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HELSINKI 1960
TILGMANNIN KIRJAPAINO

Einige Resultate der Vogelzugforschung im ostbaltischen Gebiet

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Eesti NSV Tead. Akad. Zooloogia ja Botaanika Instituut, Tartu

Das geographische Gebiet des Ostbaltikums, das hauptsächlich das Territorium Estlands, Lettlands und Litauens umfasst, ist ornithologisch gut durchforscht. Im Verlauf von fast 200 Jahren sind in diesem Gebiet ständig Vögel beobachtet worden, wobei seit der Mitte des vorigen Jahrhunderts auch dem Vogelzug Beachtung geschenkt worden ist. Anfangs waren es ornithophänologische Beobachtungen, die hauptsächlich von Laienornithologen angestellt wurden. Seit dem Jahre 1910 werden in Estland Vögel beringt. Die Vogelzugforschung wird auch noch heute in diesen beiden Richtungen fortgesetzt.

Viel weniger Beachtung hat bei uns die Erforschung des sichtbaren Vogelzugs durch unmittelbare Beobachtung gefunden. In vielen lokalfaunistischen Arbeiten finden sich wohl diesbezügliche Anmerkungen, jedoch fehlen darüber noch grössere Zusammenfassungen. Erst in den Nachkriegsjahren begann sich die Lage auf dem Gebiet der Erforschung des sichtbaren Vogelzuges zu bessern, und in den letzten Jahren in beschleunigtem Tempo.

Im Frühjahr 1953 begann die zum Institut für Zoologie und Botanik der Akademie der Wissenschaften der Estnischen SSR gehörende ornithologische Station Puchtu an der Westküste Estlands ihre Tätigkeit. Die neue ornithologische Station machte sich die Erforschung des Vogelzuges zur besonderen Aufgabe. Auf der im Frühling 1954 in Tallinn stattgefundenen II. Baltischen Ornithologenkonferenz wurde die Frage der Schaffung spezieller Beobachternetze zur Erforschung des Vogelzuges aufgeworfen. Das erste derartige Beobachternetz, das aus 9 Beobachtungspunkten in Estland und einem Beobachtungspunkt in Litauen bestand, nahm seine Arbeit schon im Herbst desselben Jahres auf.

Ein weiterer Schritt zur Vertiefung der Vogelzugforschung im Baltikum war die Gründung der Baltischen Kommission zur Erforschung des Vogelzuges im März 1955, die seither alle einschlägigen Arbeiten im ostbaltischen Gebiet organisiert und koordiniert. Von Mitte September bis Mitte Oktober 1956 wurde von besagter Kommission ein ausgedehnteres Vogelzugbeobachternetz geschaffen, das aus insgesamt 22 einzelnen Punkten bestand: 12 Beobachtungspunkte in Estland, ein Punkt in Lettland, ein Punkt in Litauen, ein Punkt am Weissen Meer, ein Punkt im Pskower

Gebiet, drei Punkte auf der Kurischen Nehrung und drei Punkte in Norddeutschland. Im Unterschied zu vielen anderen Beobachternetzen, wo Beobachtungen nur Sonntags angestellt werden, arbeiten alle Punkte unseres Beobachternetzes jeden Tag, selbstverständlich zu ein und derselben Zeit und auf Grund einer einheitlichen Methodik. Diese Methodik unterscheidet sich nicht wesentlich von derjenigen, die in Westeuropa bei analogen Beobachtungen Anwendung findet.

Zugleich mit diesen internationalen Beobachternetzen sind in den letzten Jahren in Estland auch auf enger begrenztem Gebiet Beobachternetze geschaffen worden, und zwar in der Umgebung der ornithologischen Station Puchtu. So arbeiteten z. B. auf diesem Territorium im Jahre 1955 fünf Beobachtungspunkte von Anfang August bis Mitte Oktober und 1957 neun Beobachtungspunkte von Mitte September bis Mitte Oktober.

Es muss darauf hingewiesen werden, dass in den letzten Jahren auf ostbaltischem Gebiet hauptsächlich der Herbstvogelzug untersucht worden ist, während der Frühjahrszug geringere Beachtung gefunden hat. In diesem Zusammenhang seien die im Jahre 1958 in der zweiten Hälfte des Monats Mai im Gebiet der Rigaer Bucht an mehreren Beobachtungspunkten angestellten Beobachtungen des Durchzugs von Wasservögeln erwähnt.

Aus allen diesen Forschungen geht hervor, dass der Vogelzug im Ostbaltikum nicht als ein einheitlicher Prozess betrachtet werden kann, der an allen Beobachtungspunkten dieselbe arten- und zahlenmässige Zusammensetzung hat. Sogar zwei nahegelegene Punkte können in dieser Hinsicht merkliche Unterschiede aufweisen. Die Verteilung des Vogelzuges hängt in hohem Masse von der Topographie der Landschaft ab, z. B. von der Verteilung von Wasser und Land, der Form und Richtung der Küstenlinie, dem Verhältnis von Wald und offener Landschaft usw. Das Gesamtbild des Zuges ist im Norden des Gebiets (die Westküste Estlands und die Inselgruppe) viel komplizierter als im Süden (das Gebiet des Kurischen Haffs), was unmittelbar durch die starke Gliederung der estnischen Küste bedingt ist.

Es ist bezeichnend, dass der besondere Charakter des Herbstzuges im südlichen Teil des Ostbaltikums durch Sperlingsvögel unterstrichen wird, im nördlichen Teil jedoch durch Wasservögel. Deutsche Autoren betrachten die Kurische Nehrung als die wichtigste Leitlinie des Vogelzuges in Nordeuropa. In bezug auf Sperlingsvögel trifft das zu, da sie an den von Nordost nach Südwest sich erstreckenden schmalen Landstreifen im südöstlichen Teil der Ostsee gebunden sind, der vollständig mit der allgemeinen Richtung des Herbstzuges zusammenfällt.

Etwas Analoges kann beim Durchzug von Wasservögeln in den Meerengen Westestlands beobachtet werden, mit dem Unterschied jedoch, dass hier gerade die schmalen Wasserstreifen — die Meerengen — einen starken Einfluss auf die Flugwege der Vögel ausüben. Natürlich überfliegen Wasservögel bei ihrem Zuge auch Festland, jedoch bevorzugen sie, wenn sich ihnen die Möglichkeit bietet, Wasserstrassen. Ein solches Verhalten kennzeichnet vor allem Seetaucher, Tauchenten und eine Reihe anderer Wasservögel.

Beobachtungen des Herbstzuges haben erwiesen, dass es ausser dem Gebiet des Kurischen Haffs im Ostbaltikum noch einige andere Stellen gibt, wo der Durchzug von Sperlingsvögeln zahlreich ist. Obgleich diese Orte keine so hohen Durchzugszahlen aufzuweisen haben wie das Gebiet des Kurischen Haffs, sind sie doch bemerkenswert: die Spitze der Halbinsel Sõrwe auf Saaremaa (Oesel), die Puise-Landzunge an der Westküste Estlands, die Insel Kichnu in der Rigaer Bucht und manche andere. Alle diese Punkte sind entweder weit ins Meer hineinreichende Halbinseln oder Inseln, von wo aus die Sperlingsvögel, um ihren Herbstzug in SW-Richtung fortsetzen zu können, gezwungen sind, aufs Meer hinauszufliegen.

Nach den Angaben von Waitkevicius u. a. Ornithologen, die in den letzten Jahren im Gebiet des Kurischen Haffs gearbeitet haben, beläuft sich die Gesamtzahl der dort an mehreren Beobachtungspunkten während der Herbstsaison durchziehenden Vögel auf eine Million oder mehr, davon sind 84—90 % Sperlingsvögel, von denen wiederum Finkenvögel die grosse Mehrheit bilden.

Beobachtungen sind auch an der Südküste der Rigaer Bucht angestellt worden — hauptsächlich im Herbst, zum Teil aber auch im Frühjahr —, aus denen hervorgeht, dass der Durchzug hier viel geringer ist, jedoch in seiner Hauptmasse auch aus Sperlingsvögeln besteht. Dabei ist von Interesse, dass an der Südküste der Rigaer Bucht auch der Frühjahrszug der Sperlingsvögel recht lebhaft vor sich geht, was von den meisten Punkten nicht gesagt werden kann.

Die artenmässige Zusammensetzung der Sperlingsvögel variiert während des Zuges nicht nur nach den einzelnen Gebieten, sondern auch nach der Saison. So sind beispielweise im nördlichen Teil des Ostbaltikums auf dem Durchzug im August Schwalben in der Überzahl, im September und Oktober aber Finkenvögel, Lerchen oder Bachstelzen, je nachdem, ob es sich um eine waldige oder offene Landschaft handelt.

Hinsichtlich des Vogelzuges gehört das ostbaltische Binnenland zu den ärmsten Gebieten. Der Zug zerstreut sich hier auf ein weites Territorium, und Massenansammlungen von Vögeln sind selten. Es kommt jedoch oft zu Konzentrationen in Küstengebieten, wo die Binnenlandvögel sich an der Küstenlinie gleich wie hinter einer Barriere sammeln, um dann entlang der Küste in südlicher Richtung weiterzuziehen.

Der Herbstvogelzug im Ostbaltikum ist in der Zeit von Mitte September bis Ende Oktober am regsten. Die Hauptmasse der Sperlingsvögel zieht hier in der letzten Dekade des September und in der ersten des Oktober durch. Es ist bemerkenswert, dass die Kulmination des Durchzugs einer Reihe von Sperlingsvogelarten (besonders von Finkenvögeln) auf dieselben Tage fällt. Dagegen fallen die Tage des lebhaftesten Durchzuges von Sperlingsvögeln mit denen der Wasservögel meist nicht zusammen, was darauf schliessen lässt, dass die Intensität des Durchzuges dieser beiden Gruppen nicht durch dieselben Faktoren bedingt ist.

Beim Durchzug der Wasservögel im Ostbaltikum treten einige besondere Charakterzüge zutage, die wir hier kurz behandeln wollen.

Es ist bekannt, dass der Durchzug von Tauchenten (Eisenten, Trauerenten, Bergenten u. a.) an einigen Stellen der südfinnischen Küste sehr rege ist, besonders

im Frühjahr. Die neuesten Forschungen stellen dasselbe auch an der estnischen Küste des Finnischen Meerbusens und in den westlichen Meerengen Estlands fest, wo während einer Saison Millionen Tauchenten und Zehntausende Seetaucher durchziehen. Der Frühjahrszug dieser Vogelarten ist nicht weniger lebhaft als der Herbstzug, zuweilen ist die Zahl der durchziehenden Vögel im Frühjahr sogar grösser als im Herbst.

Ein Beobachtungsposten auf der Lohusalu — Landzunge an der Küste Nordestlands notierte von Mitte September bis Mitte Oktober 1956 den Durchzug von Hunderttausenden Eisenten und Zehntausenden Trauerenten. Hierbei wurden die Beobachtungen im Laufe von 4 Stunden am Morgen und 4 Stunden am Abend angestellt.

An der Küste Westestlands am Suurväin-Sund, der das Festland Estlands von seiner westlichen Inselgruppe trennt, verläuft der Durchzug von Tauchenten noch reger. An Massenzugtagen können Zehntausende von durchziehenden Schellenten und Bergenten täglich beobachtet werden, wobei die Feststellung ihrer genauen Anzahl (besonders bei der Schellente) mit Schwierigkeiten verbunden ist.

Als zahlreichste Durchzügler über den Suurväin-Sund sind sowohl im Herbst als auch im Frühjahr die Eisente und die Trauerente, begleitet von einer geringeren Anzahl von Samtenten, anzutreffen. Die Individuenzahl der beiden erstgenannten Arten kann während einer Durchzugssaison eine Million überschreiten. Der Durchzug beider Arten beginnt im Frühjahr im April, jedoch der Massenabzug aus der Meerenge setzt in der zweiten Hälfte des Monat Mai ein. Im Laufe eines Abends können auf der ornithologischen Station Puchtu bis 200,000 Trauerenten und eine etwas geringere Anzahl von Eisenten auf dem Durchzug gezählt werden. Es ist typisch, dass diese beiden Arten im Frühjahr zusammen durchziehen können.

Der Rückzug der Trauerente setzt schon frühzeitig ein und wird im Suurväin-Sund von alten Männchen in der zweiten Hälfte des Juli eröffnet. Auch im September und Oktober ist dieser Vogel zahlreich anzutreffen, jetzt jedoch in Gesellschaft der Eisente. Während die Eisente wie auch die Trauerente im Frühjahr über den ganzen Suurväin-Sund ziehen, konzentriert sich ihr Herbstzug nun auf den mittleren Teil der Meerenge.

Massendurchzügler über den Suurväin-Sund sind auch zwei Seetaucherarten — der Prachttaucher und der Sterntaucher. Dank den Untersuchungen der ornithologischen Station Rossitten liegt eine recht gute Übersicht über den Polartaucherduchzug im Gebiet des Kurischen Haffs vor und eine Reihe diesbezüglicher Aufsätze ist im Druck erschienen (Schüz). Auch auf dem Suurväin-Sund in der Umgebung der ornithologischen Station Puchtu ist diese Seetaucherart nicht nur im Frühjahr, sondern auch auf dem Herbstzug zahlreich vertreten. Die Untersuchungen der letzten Jahre haben erwiesen, dass zusammen mit dem Polartaucher hier aber auch der Sterntaucher in grosser Zahl durchzieht. Je mehr der Frühjahrszug sich seinem Ende nähert, desto mehr beginnt gerade die letztere Art beim Durchzug zu dominieren, bis sie Ende Mai und Anfang Juni vollkommen vorherrschend ist. Es muss darauf

hingewiesen werden, dass bei bewölktem und nebligem Wetter es im Frühling und im Herbst nicht leicht fällt, diese Taucherarten in Freien voneinander zu unterscheiden, wodurch zuweilen die zahlenmässigen Angaben über das Verhältnis der beiden Arten ungenau bleiben.

Im Herbst des Jahres 1956 wurde im Laufe eines Monats auf der Lohusalu-Landzunge an der Küste Nordestlands (8 Beobachtungsstunden täglich) der Durchzug von mehr als 8,000 Seetauchern festgestellt. Am Suurväin-Sund an der Küste Westestlands setzt der Seetaucherdurchzug Ende April oder Anfang Mai ein. Während der ganzen Saison ziehen über 10,000 Seetaucher durch, wobei sich das Maximum auf 1,200 Individuen täglich beläuft. Der Massendurchzug im Herbst findet in der zweiten Dekade des September und in der ersten des Oktober statt, wobei während der ganzen Saison bis 15,000 Individuen notiert werden und das Tagesmaximum 2,000 Individuen beträgt (z. B. am 22. September 1957).

Wie die Trauerente und die Eisente, so ziehen auch die Seetaucher im Frühjar über den ganzen Suurväin-Sund, während im Herbst ihr Durchzug sich mehr in der Mitte der Meerenge konzentriert.

Was die grossen Binnengewässer des Ostbaltikums betrifft, so ist der Vogelzug am Wõrtsjärw-See gering, desto beachtenswerter ist er jedoch am Peipsi-See. Dort finden sich während der Zugsaison Vogelarten ein, die gewöhnlich nur am Meer vorkommen und sich nur selten ins Binnenland verirren (Ringelgans, Trauerente, Eisente, Mantelmöwe, Austernfischer, Steinwälzer u. a.).

Wertvolle Angaben über den Vogelzug am Peipsi-See hat der estnische Ornithologe L. Rootsmäe durch seine Beobachtungen im Mustwee am nordwestlichen Ufer des Sees zusammengetragen. In der letzten Dekade des Juli zieht die Trauerente in grosser Zahl über den See. Der Entendurchzug erreicht sein Mazimum Ende September und im Oktober, wobei die Hauptdurchzügler Bergenten, Eisenten und Schellenten sind. Von den Schwimmenten nimmt die Stockente zahlenmässig die erste Stelle ein und ist hauptsächlich im August und September anzutreffen.

Im südlichen Teil des Peipsi-Sees — am Pskower-See — stehen von den Enten im Herbst die Schellente, Bergente und Reiherente an ersten Stelle, aber auch Schwimmenten sind recht zahlreich vertreten.

Wie aus dem Vorhergehenden zu ersehen ist, geben Sperlingsvögel und Wasservögel dem Vogelzug im Ostbaltikum das Gepräge — die ersteren im südlichen, die letzteren im nördlichen Teil des Gebiets. Eine nur annähernd so hohe Individuenzahl wie bei den vorstehend genannten können wir bei keiner anderen Vogelordnung feststellen.

Der Durchzug von Limicolen beginnt im Ostbaltikum Ende Juni und erreicht seinen Höhepunkt im Juli und August. Für den Durchzug dieser Vögel sind geeignete Rastplätze an den Ufern der Gewässer von grosser Wichtigkeit. Die letzteren hängen ihrerseits vom Wasserstand ab. Diese lokalen wie auch andere fernerliegende Ursachen bedingen jähe Schwankungen in der Zahl der Limicolen in den einzelnen Jahren. Im allgemeinen finden sich an den Meeresküsten des Ostbaltikums und an

den Binnengewässern bei weitem nicht so viele Schnepfenvögel wie beispielsweise auf Süd-Öland. Die zahlreichsten durchziehenden Limicolen an unseren Küsten sind Kampfläufer, Alpenstrandläufer, Sandregenpfeifer, Kiebitze und einige andere. Im Herbst kommen Limicolen immer zahlreicher vor als im Frühjahr, mit Ausnahme des Grossen Brachvogels und des Austernfischers, die im Frühjahr zuweilen in Schwärmen erscheinen, im Herbst aber meist einzeln ziehen.

Möwen überfliegen in recht beträchtlicher Zahl die Meeresküsten wie auch die Binnengewässer. Im Herbst rasten grosse Scharen von Möwen (Lach- und Sturmmöwen) auf den weiten Feldern Mittelestlands (in der Umgegend von Tartu, Jõgeva und Põltsamaa). Es ist recht schwer, den direkten Möwendurchzug an der Meeresküste zu verfolgen, da ihre Flüge meist einem ziellosen Umherstreifen gleichen (besonders bei der Mantelmöwe, während der Zug der Heringsmöwe organisierter verläuft). Interessant ist der Zug der Raubseeschwalbe. Schon in der Mitte des Sommers erscheinen an den Binnengewässer Estlands einzelne Individuen und auch kleine Schwärme. Viele dieser Vögel tragen finnische Ringe. Gegen den Herbst wächst die Zahl der Raubseeschwalben nach und nach, bis sie im September nach der Monatsmitte verschwinden.

Der Durchzug anderer Vogelarten ist im Ostbaltikum verhältnismässig gering. Das gilt vornehmlich von Raubvögeln. Tauben ziehen in grösseren Mengen durch den südlichen Teil des Gebiets, im nördlichen findet ihr Durchzug während eines kurzen Zeitabschnitts Ende September und Anfang Oktober statt, wo auch hier grosse Schwärme anzutreffen sind.

Zwecks Untersuchung des sichtbaren Vogelzuges im Ostbaltikum sind von der Baltischen Kommission zur Erforschung des Vogelzuges Massnahmen getroffen worden, die eine ununterbrochene Arbeit der Beobachternetze gewährleisten. Im September 1957 wurde auf der ornithologischen Station Puchtu ein Seminar für Vogelzugsforscher abgehalten, das sich die Vereinheitlichung der Beobachtungsmethodik und die Vermittlung von praktischen Erfahrungen bei der Erforschung des sichtbaren Vogelzuges zum Ziel setzte.

Im Herbst des Jahres 1958 — vom 16. September bis zum 15. Oktober — plant die Baltische Kommission zur Erforschung des Vogelzuges nächstfolgende Vogelzugbeobachtungen anzustellen und dieses Mal schon auf ausgedehnterem Territorium. Nicht nur den ostbaltischen Ornithologen und den Ornithologen der angrenzenden Sowjetgebiete, sondern auch finnische, schwedische, dänische, deutsche und polnische Ornithologen sind aufgefordert worden, sich an der Arbeit des besagten internationalen Beobachternetzes zu beteiligen. Die meisten Personen und Anstalten, an die man sich in dieser Angelegenheit gewandt hat, haben ihre Beteiligung zugesagt.

Es bleibt nur zu wünschen übrig, dass die für diesen Herbst vorgesehenen Zugbeobachtungen erfolgreich verlaufen und unsere Kenntnisse auf dem Gebiet des Vogelzuges im Ostseereaum und am Weissen Meer in bedeutendem Mass bereichert werden.

Remarks on the Breeding Seasons in the *Tubinares*, particularly of the North Pacific

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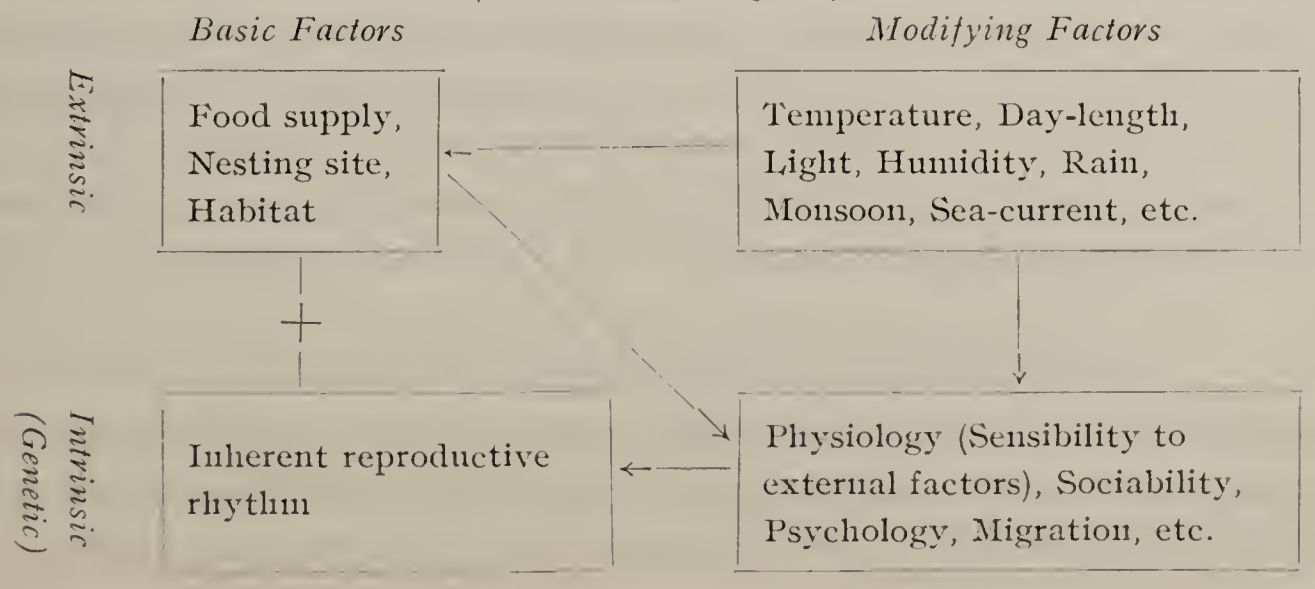
INTRODUCTION

If a bird with a healthy inherent reproductive cycle is provided with adequate food and nesting site under favourable condition, it would be potentially capable of breeding unseasonally, as in domestic fowl. These are basic, and necessary, factors. In natural conditions, various complexes of modifying factors affect the above fundamental factors: at high latitudes, temperature is apparently a limiting factor, while in Temperate Zones the day-length (usually increasing but sometimes perhaps decreasing) is the most important factor in many birds, particularly the Passerines. In the Tropics rain and light (ultra-violet) become important. These external modifying factors act upon birds directly or through the influence on food supply and environment, while the bird's innate sensibility to these external stimuli and other innate factors, such as sociability, migration, etc. are important factors which modify the timing of inherent reproductive rhythm. These correlations have been discussed by many authors and may be diagrammatically suggested by the following table:

TABLE 1

Factors determining the breeding seasons
(A theoretical diagram)


Basic Factors
Modifying Factors
Extrinsic
Food supply, Nesting site, Habitat
Temperature, Day-length, Light, Humidity, Rain, Monsoon, Sea-current, etc.
Intrinsic (Genetic)
Inherent reproductive rhythm
Physiology (Sensibility to external factors), Sociability, Psychology, Migration, etc.

The effects of various factors are of complex nature and may vary by species, races and even populations. I shall not discuss each of these factors, but I shall rather emphasize the effect of temperatures in a group of pelagic birds, the *Tubinares*.

THE REVERSAL OF BREEDING SEASON IN THE NORTH AND SOUTH

As shown by table 2, the reversal of breeding season in the northern and southern hemispheres is conspicuous in the *Tubinares*, being of world-wide distribution. In the South Seas, the low summer temperatures are not decisively inhibitory even in such a high latitude as New Zealand. Thus, the breeding season in the South Seas is generally more prolonged than in the corresponding northern seas, and we do find some exceptional summer breeders. The northern limit of winter September—February breeding is found in Torishima about 30° north in Izu Islands, Japan, in the North Pacific, and Bermuda about 32° north in the North Atlantic. The southern limit of March to August breeding reaches 30—40° south in the Australian and Tristan da Cunha waters, and on Kerguelen (in *Pterodroma macroptera*) nearly 50° south.

TABLE 2

The reversal of breeding season by sea-zones in the Tubinares

No. of species with known breeding season by sea-zones	*Breeding season* (Egg dates)		
	Summer	Summer and winter	Winter
1. Arctic to N. Temperate Zone			
8 species and races	8	0	0
2. N. Subtropical Zone			
28 species and races	15	7	6
3. Tropical Zone			
16 species and races	8	6	2
4. S. Subtropical and S. Temperate Zones to Antarctica			
51 species and races	3	3	45

(Summer includes the months, March to August, and winter, September to February.)

The reversal of breeding season in the north and southern hemispheres is easily demonstrated in introduced birds, though some birds such as the Emu retain the original cycle even if introduced into the northern hemisphere. The seasonal reversal of breeding cycle can thus be regarded as the reproductive acclimatization caused by specific sensibility to the similar threshold of external stimulation involved in the reversed season. A good example of the reversal of breeding season in the north and south in a single species has been demonstrated in *Puffinus pacificus* by Dr. MURPHY.

EFFECT OF DAY-LENGTH AND TEMPERATURE ADAPTATION

The winter breeding of the North Pacific albatrosses does not agree with the day-length theory of breeding, and the effect of daylength is confusing in the *Tubinares* in general. Non-migratory southern species, as well as northern temperate zone

species, breed with increasing day-length, while long-distance migrants, such as *Puffinus tenuirostris*, start southward in autumn from northern seas with decreasing day-length to breed in the southern hemisphere, where they then experience the increasing day-length. A few northern subtropical species breed in winter, therefore with decreasing day-length. There might be birds, particularly non-passeres, which are insensitive to day-length or sensitive to decreasing day-length, as shown in some mammals. (Dr. WOLFSON at this Conference reported the need of autumnal decreasing day-length for the junco to react to the increasing day-length in the spring.)

On the other hand, a sensibility to temperature in North Pacific albatrosses is evident, and this might be responsible for their winter breeding. *Diomedea immutabilis* is rather a cold-adapted species, and arrives off Japan in March when the sea is still cold and *D. nigripes* follows it, arriving in April or May. In these months, the temperatures of this sea area are: air about 8—15° and water 10—15 or 17° C. From my records taken off north Japan to the Bering Sea in June, *nigripes* showed preference for air 17—22°, water 10—16° C (also cf. THOMPSON, Auk, 1951) and *immutabilis* air 13—15° and water 10° C. During the breeding season of these species both air and water temperatures in Torishima waters are below 20° C (the lowest being air 14° and water 17° C), and there is a marked increase in temperature from May or June to October or November, during which the birds are absent from the island. In the Bonin Is. where *nigripes* breeds, this increase of temperatures is recorded also from April or May to November or December. The same can be said for the air temperature of Midway waters, the center of their breeding range.

CORRELATION OF FOOD SUPPLY

In the *Tubinares*, we find the summer or winter breeding cycle sometimes prevail on an island. In the Galapagos Is., except for *Puffinus lherminieri subalaris* which has a prolonged breeding season, the five other *Tubinares* are all restricted spring breeders. LACK (1950) considered this to be correlated with the seasonal approach of the cool Humboldt Current bearing marine food. The five species, I would suggest, may be cool-acclimatized species and therefore feed on the Humboldt Current, which regulates their breeding season to the spring, while *Puffinus lherminieri subalaris* is resident, being warm-adapted, and shows irregularity of egg dates. Torishima has had four species, *Diomedea albatrus* (some at present), *D. immutabilis* (none at present), *D. nigripes* (a few) and *Oceanodroma tristrami*, which were all winter breeders. Here, too, temperature adaptation should be an important factor and is supported by food factor condition. The temperature adaptation is inherent and when not supported by food availability the species would die out. Thus, the temperature adaptation is the primary or fundamental factor while food is a necessary factor. The above species migrate north to Japanese waters in spring, and the principal food of these albatrosses are squids, chiefly *Ommastrephes*, which prefers also the water temperature zone of 15° C. The squids are the right size (about ten cm.)

as food, forming one of the abundant foods of the *Tubinares*, porpoises and fur seals. They have grown too large for birds, even albatrosses, to swallow by autumn or winter when they are caught for human food. On Torishima, during the winter breeding season, the albatrosses also feed chiefly on squids, which they seem to obtain not far from the island, but adequate information about the seasonal movement of squids is not yet available.

CORRELATION WITH MIGRATION

As referred to above, the post-breeding northward movement in spring of North Pacific albatrosses from their subtropical breeding islands may be the result of their cold-acclimatization, with favourable condition of the food supply. Two species of Storm Petrels, *Oceanodroma tristrami* and *O. matsudairae*, breed on the North Volcano I. and the breeding season is about two and half months delayed in the latter species. *Tristrami* arrives in late October and lays eggs in late January or early February, leaving the island in early April, while *matsudairae* arrives in mid or late January, laying eggs in late March or early April and leaves in mid-June. This is of interest showing the correlation between breeding season and migration, for the spring-breeding *matsudairae* is a more warm-adapted species as it is a casual visitor north to Japanese waters, where the winter-breeding *tristrami* regularly summers. This kind of movement is secondary and is subject to temperature adaptation, while the longdistance migration of some southern shearwaters are of inherent nature and may control the breeding season as FALLA has found in the New Zealand species.

SOME CORRELATIONS WITH EVOLUTION

The reproductive rhythm may be retained unless a change is forced upon it by external factors. We find spring breeding or summer and winter breeding prevailing over winter breeding in the tropics, where the original cycle could be retained because of the uniform climate, and this might suggest the northern origin of such tropical species. Also, one might suspect that the few winter-breeding northern species have evolved from the South Sea population where winter-breeding is the rule.

Oceanodroma tristrami is unique as a winter breeder among the members of its tribe, which are all spring breeders. Its winter cycle has therefore been derived from a spring cycle, as a result of its physical adaptation to a cool oceanic environment and consequent summer movement to the north. The winter cycle of the northern albatrosses may be explained in two ways. One, that thay are of southern origin and retain the original winter cycle. Two, that they are originally northern Temperate Zone species, but a lack of suitable islands forced them to breed on subtropical islands. Their innate physiological adaptation to a cooler zone has established their winter breeding cycle. HUTTON (1865) first suggested their southern origin, but later (1903) believed their North Atlantic origin, pointing out the European fossil evidence and primitive plumage characters of northern albatrosses, particularly *D. nigripes*.

The following remark may be added here. *D. irrorata* is the only tropical albatross breeding on Galapagos Is. in spring (egg dates May and June) and it is most related to *D. albatrus* of the North Pacific from which it differs in not having distinct juvenile plumage, while it is also related to such South Sea species as *D. exulans* or *D. epomophora* (other South Sea species make a Mollymawk-group, *Thalassogeron*). *D. irrorata* lays its egg on bare ground as in *D. albatrus*, and other North Pacific forms make simpler nests than the South Sea forms which are all distinct nest builders. (This habit may have developed partly as a snow-adaptation (RAND, 1954)). The downy chicks of the northern forms are dark coloured (though white-breasted in *immutabilis*) and that of *irrorata* is dichromatic (pale and dark phases), while in the South Sea species chicks are distinctly whiter and the most nearly white chick is found in *D. epomophora*. In *D. exulans* the plumage is gradually whitened, and *D. albatrus* has all-dark first and half-dark later juvenile plumages, while *D. nigripes* is the only all-dark form in adult stage in the genus *Diomedea*, thus retaining this possibly primitive characteristic throughout its life. These considerations lead me to favour HUTTON's second theory that North Pacific albatrosses as well as *D. irrorata* have not evolved from the South Sea population. (An article with more fully documented evidence and more detailed reference to the literature will be published elsewhere.)

Relationship of the House Wren (*Troglodytes aedon*) of North America and the Brown-Throated Wren (*Troglodytes brunneicollis*) of Mexico

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Until 1945 the House Wren *(Troglodytes aedon)* and the Brown-throated Wren *(Troglodytes brunneicollis)* were considered allopatric species, the former representing the breeding form of the United States and Canada and the latter the resident form of the Mexican plateau. In that year, Brandt described a new subspecies, *T. b. vorhiesi*, of the Mexican form, and gave as its distribution several mountain ranges of extreme southeastern Arizona. Following this discovery, Oberholser is quoted (in Brandt 1951, p. 511) as having remarked: »Here we have two birds so similar in plumage and size that some specimens in hand are exceedingly difficult to identify, yet their nests, eggs, and notes are so entirely different that there is no doubt about their specific distinctness.» Brandt's announcement (1945), implying sympatry of the two species in Arizona, initiated a reexamination of populations of *Troglodytes* along the United States-Mexico border (Marshall 1956) and ultimately of the relationships throughout the genus (Paynter 1957).

Brandt (1945, 1951) based his discrimination between the Arizona populations of *aedon* and *brunneicollis* on three criteria: morphology, eggs, and voice. The objective of the present study was to investigate and evaluate these criteria and to interpret the results in terms of the relationship of the North American and Mexican forms. After briefly reviewing the evidence to date, I will present some additional data on the relationship of these wrens, resulting from field work conducted during 1956 and 1957.

Specimens were examined in the collections of the U. S. National Museum, the Museum of Comparative Zoology, and the American Museum of Natural History. Eggs of this genus, from the western United States and Mexico, were examined in the collection of the American Museum of Natural History.

The ranges of *aedon* and *brunneicollis* approach one another in the region shown in figure 1. During the breeding season, these birds are ecologically restricted to pine forests, which are to be found only in the higher mountain ranges. For the purpose of this discussion, then, the blackened portion of figure 1, representing elevations above 6,000', may be interpreted as

Fig. 1. Potential breeding range of *Troglodytes* in southwestern United States and Mexico, as revealed by elevations above 6,000 feet (blackened area). Numbers identify locations of wren populations studied: 1 — Sierra Huachinera, Sonora; 2 — Huachuca Mts., Arizona; 3 — Chiricahua Mts., Arizona; 4 — Santa Catalina Mts., Arizona; 5 — Pinaleno Mts., Arizona; 6 — White Mts., Arizona.

the potential breeding range of *Troglodytes* in this region. Field observations and recordings of *brunneicollis* were made in the Sierra Huachinera (No. 1 in figure 1) of Sonora, a western spur of the Sierra Madre Occidental, on May 31 and June 1, 1956. Several wren populations were visited within the presumed area of geographical overlap in extreme southeastern Arizona: the Huachuca Mts. (No. 2) on May 18 and 28, 1956; and the Chiricahua Mts. (No. 3) on May 7, 19, 20, 21, 26, 27, and June 16, 1956. Populations of *aedon* just north of Brandt's zone of overlap were studied in the Santa Catalina Mts. (No. 4) on May 12, 16, and 23, 1956, and in the Pinaleno Mts. (No. 5) on May 24 and 25, 1956. Another population of *aedon* was observed and recorded in the White Mts. (No. 6) of Arizona on June 5 and 6, 1956. For comparative purposes, additional recordings were made of the eastern North American race of *aedon* in Oxford, Ohio on May 29, 1957.

Representative songs and calls from these populations were recorded at 15 inches per second, using a VU Magnemite tape recorder and an Altec 660B dynamic microphone. Recordings from Arizona and Sonora were made with the aid of a folded reentrant horn, while those from Ohio were made with a 24″ parabolic reflector. Though the reentrant horn and parabolic reflector differ somewhat in relative performance (Lanyon 1957 b), the results are comparable for the type of analysis used here. No preamplification was used. The recordings were subsequently graphed by a sound spectrograph, a technique that has been adequately treated in a number of recent avian studies in England (Thorpe 1954, Marler 1956) and the United States (Kellogg and Stein

1953, BORROR 1956, LANYON 1957 a). The sound spectrograph used in this study was especially modified for bird song analysis, to introduce pre-emphasis while recording in the range of 8 KC to 12 KC to compensate for the loss that is introduced in the same range by the magnetic material. This results in an overall response curve that is essentially flattened. This model analyzes from 0 to 6 KC on one scale and 6 to 12 KC on another scale, necessitating a horizontal splice of graphs wherever a single sound pattern involves frequencies of both scales.

Grants from the Frank M. Chapman Memorial Fund and the American Philosophical Society (Penrose Fund) made this study possible. I am grateful to Dr. MONT CAZIER, Director of the American Museum's Southwestern Research Station, for making available to me a sound spectrograph and other equipment. I am indebted to Dr. ALLAN PHILLIPS for guiding me into the Sierra Huachinera, and to Dr. JOE MARSHALL for helpful suggestions.

RESULTS

Morphology

BRANDT (1945, 1951) recognized individuals of *T. brunneicollis vorhiesi* (from sympatric *T. aedon parkmanii*) by their »more prominent light superciliary stripe» and buffy rather than gray breast. MARSHALL (1956) investigated the extent of morphological variation in these populations and demonstrated a cline with respect to these characters: gray-flecked or whitish chested individuals in northern Arizona, having no superciliary line, to buff chested individuals in northern Mexico, having a conspicuous superciliary line. PAYNTER (1952) recognized a similar cline toward darker coloration, from north to south, in the Mexican races of *brunneicollis*. MARSHALL (1956) reported on a number of »mixed pairs» in the Rincon Mts. of Arizona, including a whitish chested male paired with a rich, buff chested female, and I have made similar field observations of mixed pairing in the Chiricahua Mts. A survey of specimens from Arizona and northern Mexico led to my own conclusion that such a cline exists. It was noted, however, that this gradient of morphological characters is definitely »steeper» in the region under discussion than it is, for example, in the intergradation zones between races of *aedon* in the United States or between races of *brunneicollis* in Mexico. PAYNTER (1957) states: »The converging of characters is . . . an indication that the groups are not specifically distinct.»

Eggs

BRANDT (1951) remarked: »It was especially upon the unlike eggs that I predicated my strongest argument.» He described the type set of eggs of *brunneicollis vorhiesi* as »about a third smaller and more sparingly marked than those of the House Wren» (BRANDT 1945). The average size of ten eggs, collected by BRANDT and believed to be *vorhiesi*, is 16.19×12.35 mm (BRANDT 1951). Measurements of 40 eggs in the United States National Museum, identified as *aedon parkmanii*, average 16.3×12.6 mm (BENT 1948). That *brunneicollis* eggs may, in fact, be larger than BENT's average for *aedon parkmanii* is demonstrated by a set of four eggs that I collected

from the Sierra Huachinera, Sonora (AMNH 17346). These averaged 17.4×13.1 mm, yet are within the extremes listed by BENT for *aedon parkmanii*. With regard to color and markings, they are within the range of variation exhibited by eggs of *aedon parkmanii* in the American Museum of Natural History collection. MARSHALL (1956) detected no color difference between a set of eggs collected in the Rincon Mts. of Arizona and a set collected in the Sierra Madre of Sonora.

Voice

I can find no published statement as to the nature of the distinction in voice between these wrens. BRANDT (1945) remarked that their voices were »similar», yet »different». After collecting the first specimen of the Brown-throated Wren from the Chiricahua Mts., PHILLIPS is quoted (in BRANDT 1951, p. 512) to have remarked: »I am very pleased to find that this bird is so distinct and to learn personally that it can be readily identified by its song.» But MARSHALL (1956), with field experience in both Arizona and Mexico, recognized no consistent difference in the voices of these wrens. Clearly, an objective analysis of voice appeared to be in order.

Probably the most characteristic call note of the House Wren is one that has been phonetically represented as a »churrr» by KENDEIGH (1941), who considered it to have the »general purpose of notifying the male of the female's presence», though it is common to both sexes. An analysis of the sound spectrograms of this call (fig. 2), recorded from widely-separated wren populations, indicated no greater variation than is to be noted among the individuals of any one population. Energy is concentrated in a frequency range of 3 to 6 KC. The average duration is .3 second, though this is subject to considerable temporal variation within the same individual and appeared to be a function of level of excitement. All of the 54 calls analyzed were composed of a series of similar elements, arranged in an overall pattern of descending frequencies (refer to fig. 2). The number of these elements varied from 7 to 17 but averaged about 12. An additional feature of uniformity was the tendency for at least

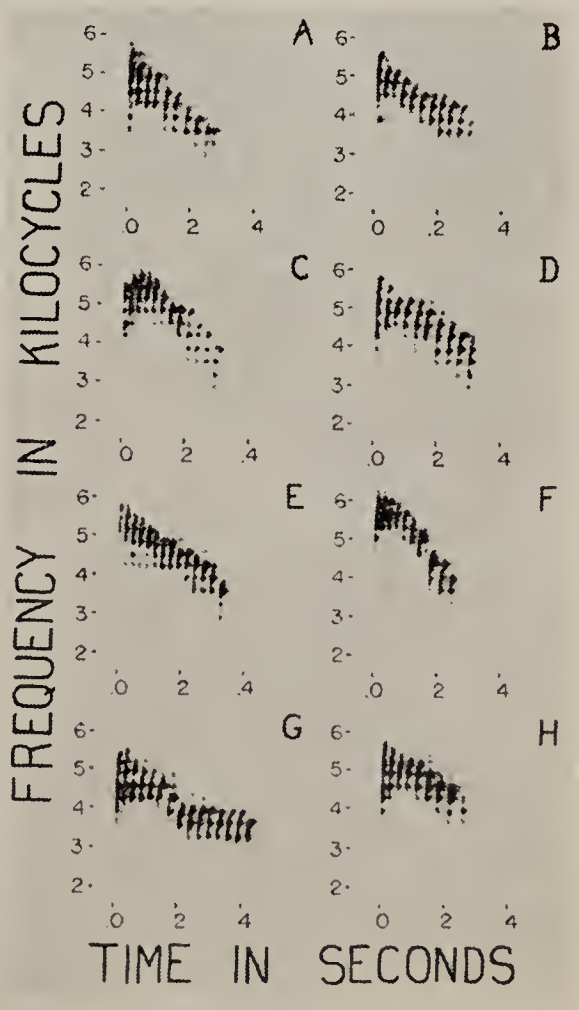

Fig. 2. Sound spectrograms of a characteristic wren call note, from recordings made in the following localities: A — Oxford, Ohio; B — White Mts., Arizona; C — Pinaleno Mts., Arizona; D — Santa Catalina Mts., Arizona; E — Pine Canyon, Chiricahua Mts., Arizona; F — Cima Trail, Chiricahua Mts., Arizona; G — Sierra Huachinera, Sonora (male no. 1); H — Sierra Huachinera, Sonora (male no. 4).

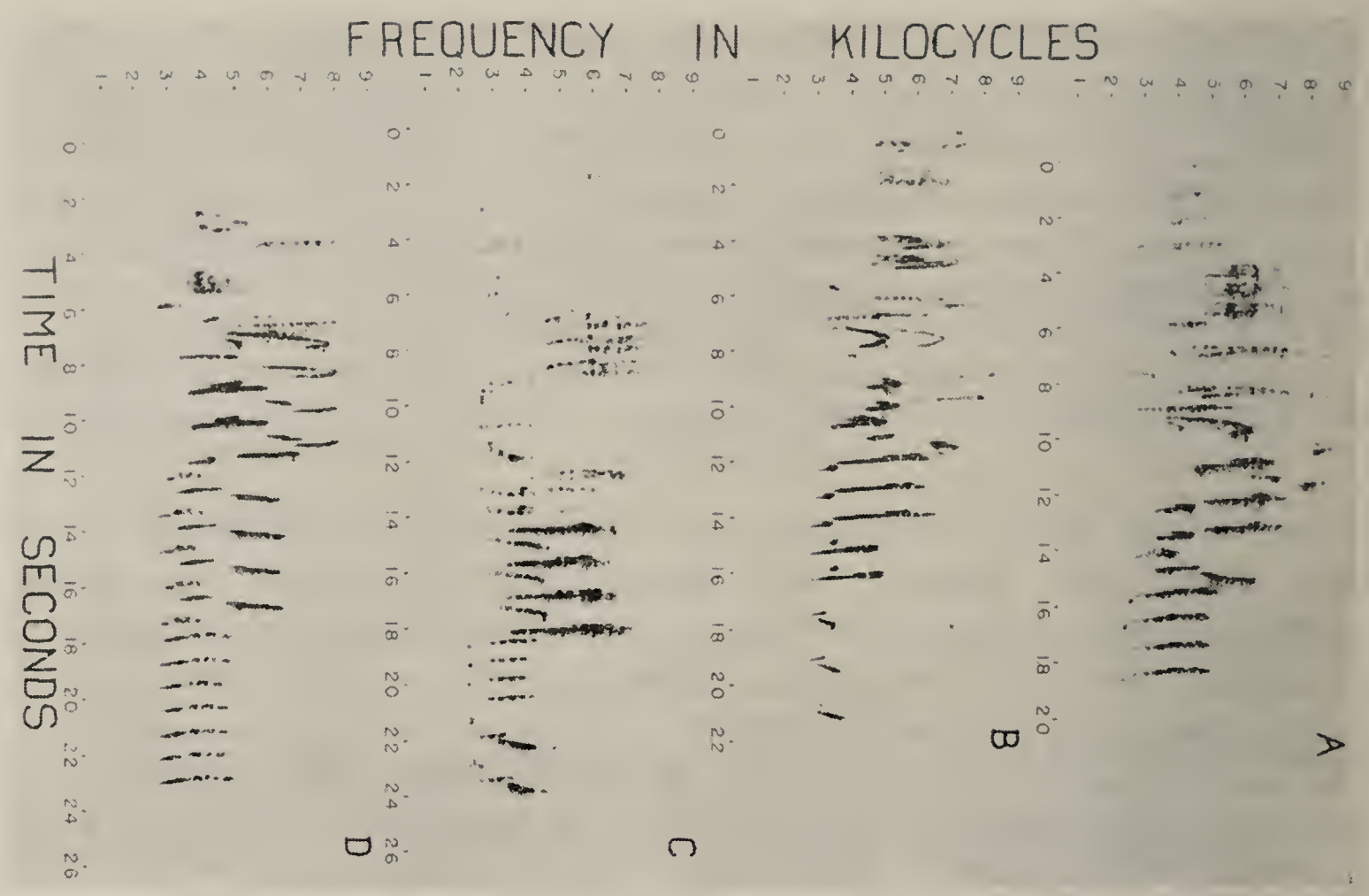

Fig. 3. Sound spectrograms of primary song, from recordings made in Oxford, Ohio. A, B, and C from male no. 1, and D from male no. 2.

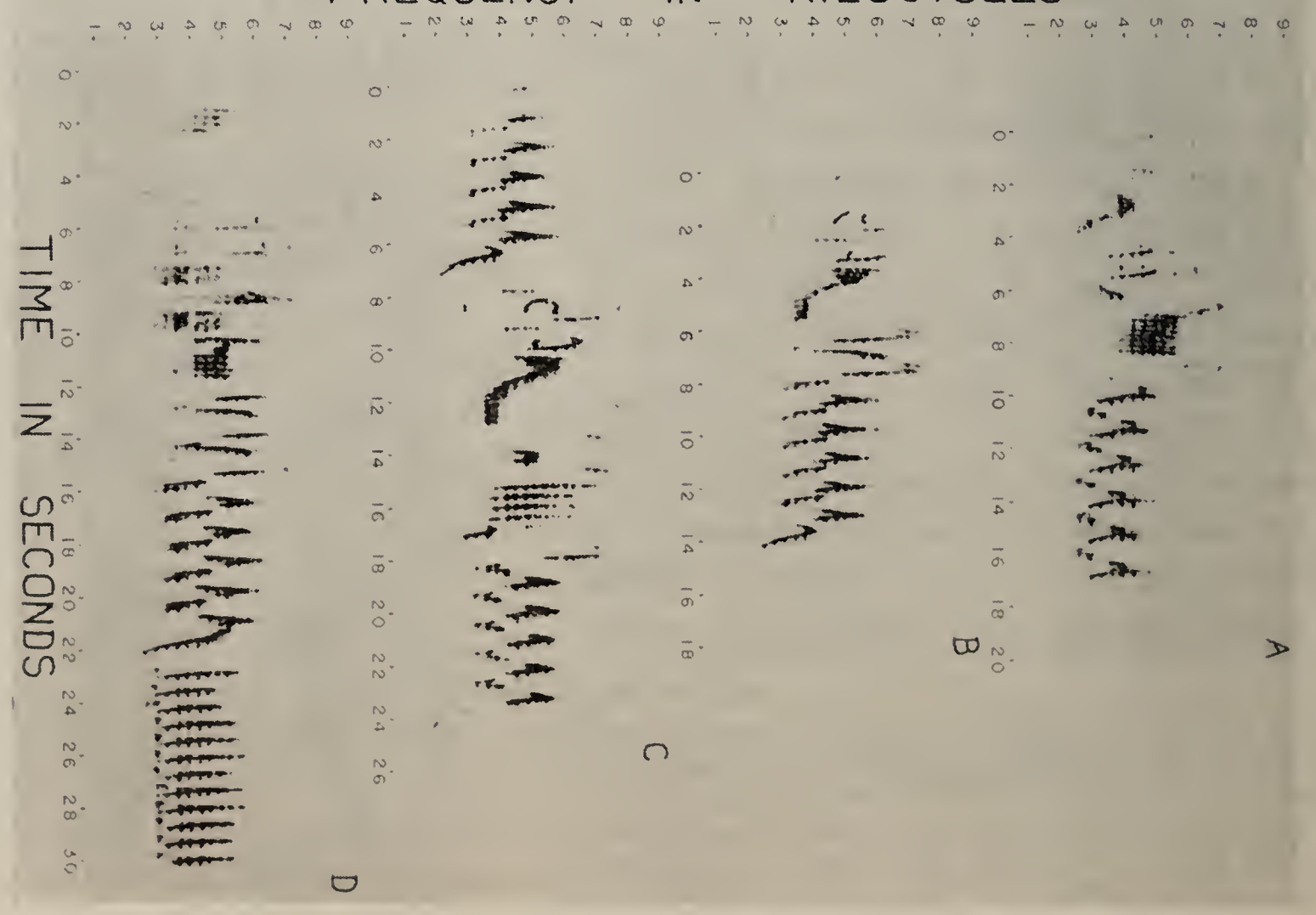

Fig. 4. Sound spectrograms of primary song, from recordings made in the White Mts. of Arizona. A, B, and C from male no. 1, and D from male no. 2.

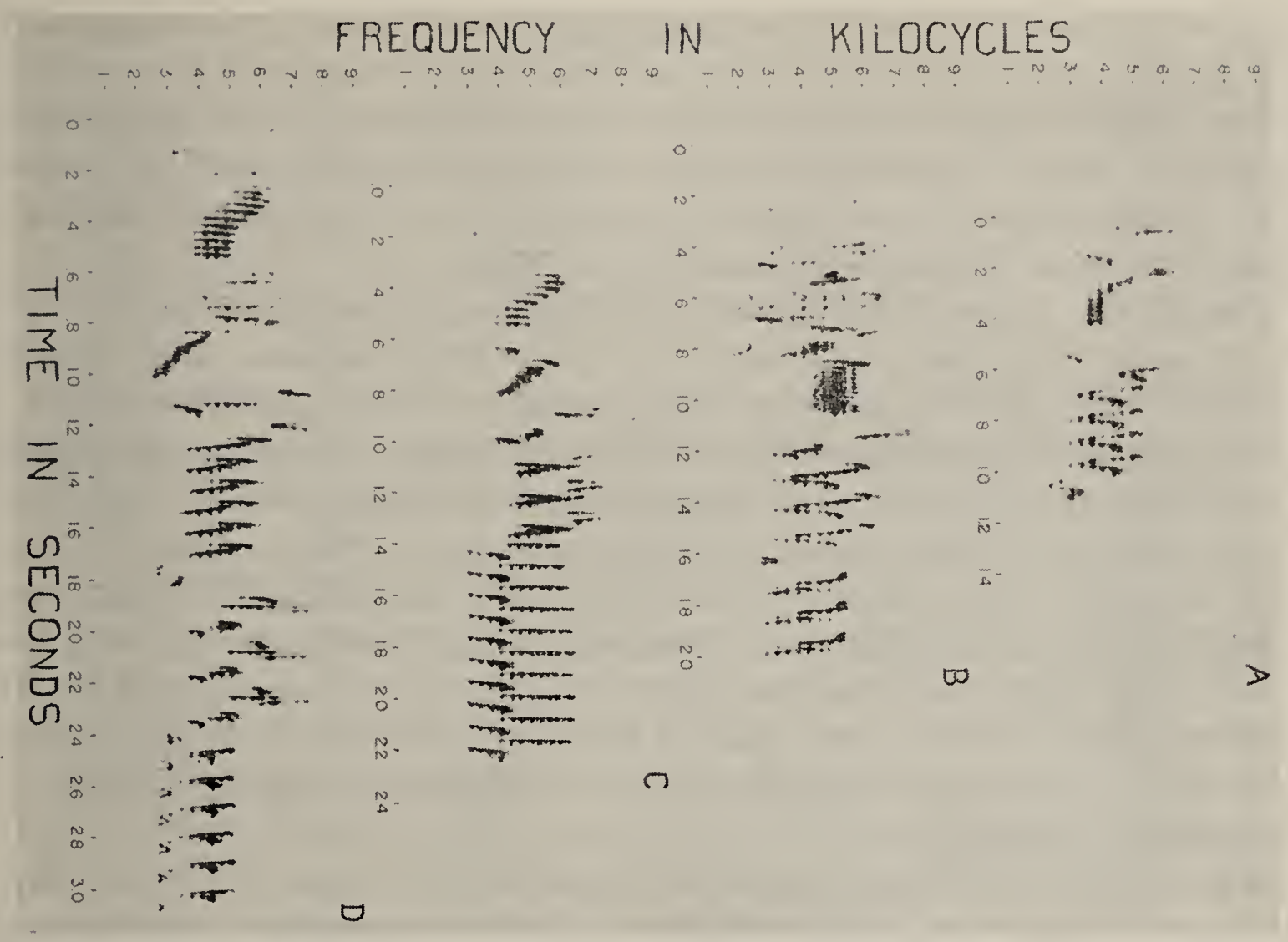

Fig. 5. Sound spectrograms of primary song, from recordings made in the Chiricahua Mts. of Arizona. A — Cima Trail; B — Barfoot Trail; C and D — Pine Canyon.

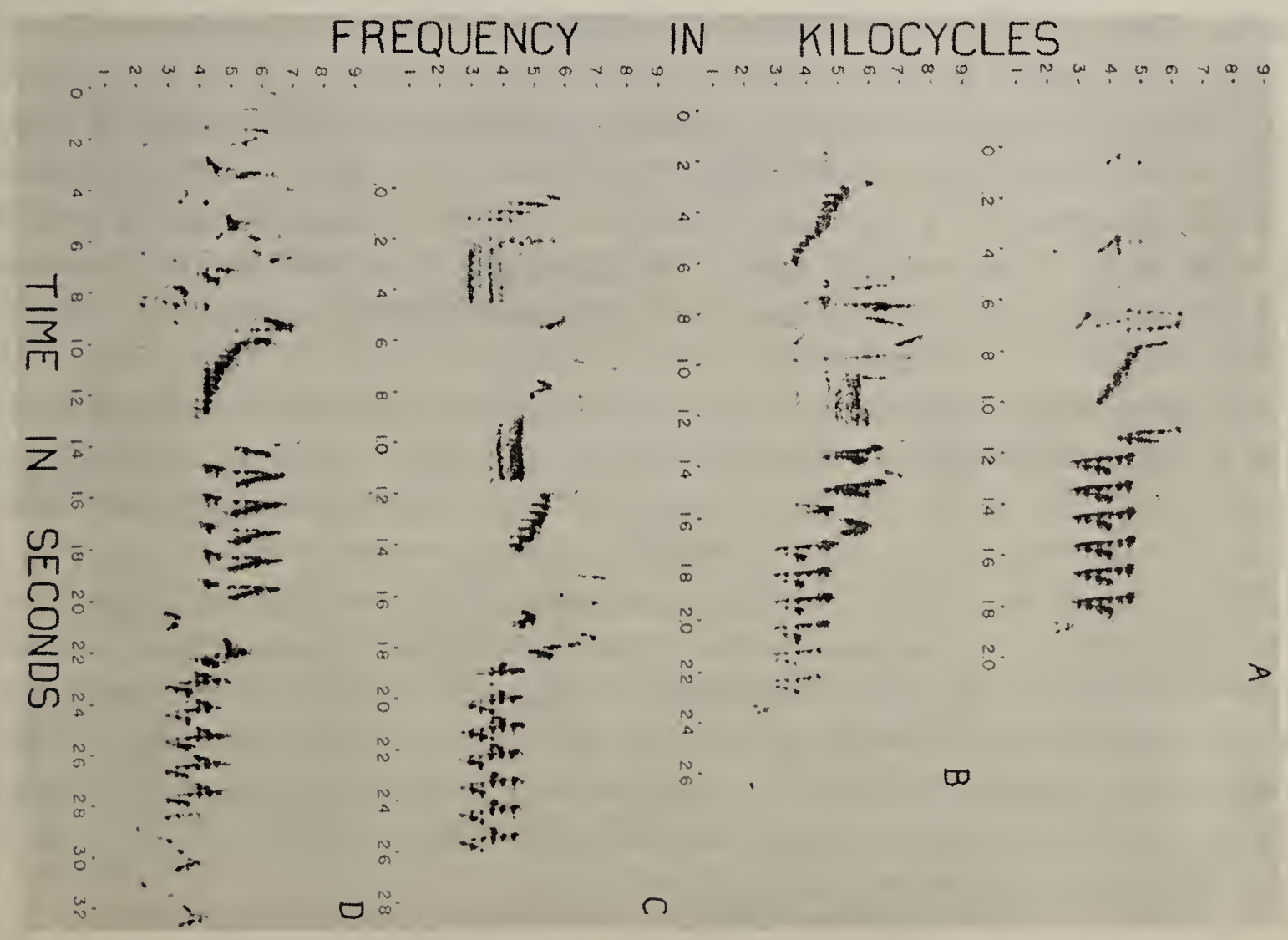

Fig. 6. Sound spectrograms of primary song, from recordings of four different individuals in the Sierra Huachinera of Sonora.

some of the elements in each call to ascend slightly in frequency, this in spite of the overall descending pattern of any given call. This feature is expressed in the spectrograms of figure 2 by the manner in which the individual elements »lean» slightly toward the reader's right. In view of these data, it is understandable that the call notes of the Mexican wrens, when I heard them in the field, sounded identical to those of the House Wrens in the eastern United States.

The primary song of the House Wren, *i. e.* the »territorial» vocalization by which the species is best known, is a loud, musical, bubbling rendition. Sound spectrograms of recordings of primary song from a number of wren populations appear in figures 3 to 6. Primary song was found to be extremely variable in any given individual and among individuals of the same population. Likewise, there was obvious variation between widely separated populations. In spite of this variability, the primary song of the House Wren is, as SAUNDERS (1951) has indicated, »of such a character that it is nearly always easily recognizable». Significantly, primary song from wren populations in the Sierra Huachinera of Sonora is at once recognized as being disinctly House Wren-like. The question has been raised whether or not there are difterences of taxonomic significance between the primary songs of Mexican and Arifzonan populations.

There was no significant difference in primary song among the various wren populations studied with respect to highest and lowest frequencies and duration of song. The individual song patterns further agreed with one another in having the greatest intensity (sound energy level) concentrated on the middle elements and the weakest intensity concentrated on the introductory elements. This extreme fluctuation of sound energy posed a problem in terms of graphing and presenting material for publication. To register the low intensity elements at the beginning of a wren's song, without distorting (»overloading») the much louder elements in the remainder of the song, necessitated separate graphing and vertical splicing of various portions of each song. These vertical splices of spectrograms, as well as the horizontal splices due to a shift in frequency scale (at about 6 KC), are apparent in figures 3 to 6.

In comparing the spectrograms of primary song with respect to detailed configuration of component elements, one finds a closer agreement between the sound patterns of the wrens of Sonora (fig. 6) and central eastern Arizona (fig. 4), heretofore considered separate species, than between the sound patterns of the Arizona (fig. 4) and Ohio (fig. 3) populations, recognized as belonging to one species. This will certainly not surprise anyone aware of the extent of intraspecific geographical variation in bird song. However, it does invalidate any use of a »difference in song» as a basis for specific distinction between *brunneicollis* and *aedon*. It is of further interest that primary song recorded from the Santa Catalina Mts. population elicited the same degree of territorial response when played back to Sonoran birds, as was given by the Sonoran birds in response to their own voice.

DISCUSSION

A normal consequence of the shift in emphasis from a morphological species concept to a biological species concept is the reexamination of the taxa determined by early taxonomists. Recent systematic appraisals of the geographic representatives of the genus *Troglodytes* are a part of this new approach. We still have too little in the way of adequate field data on comparative ethology and ecology to justify many changes.

The House Wren breeds in an essentially continuous population throughout its breeding range, with little restriction placed on gene flow between its eastern *(aedon)* and western *(parkmanii)* races.[1] Likewise, there is considerable gene flow between the five or six races of the Brown-throated Wren, which breeds in a virtually continuous population throughout the wooded mountain areas of the Mexican plateau. These two continuous ranges approach one another along the Arizona-Sonora border. At that point gene flow between the two forms is greatly restricted because of discontinuities in distribution of preferred habitat. This is reflected in the steepness of the morphological cline described above. In spite of this restricted interbreeding, no notable divergences in breeding behavior or vocalizations have been developed.

The evidence for intergradation between the North American and Mexican House Wrens brings into clearer focus the relationship between *T. aedon* and *T. musculus* of Central and South America. Chapman and Griscom (1924) ventured the prediction that »the small »distributional» gap between *musculus* and *aedon* will be closed», but did not include *brunneicollis* in this, for they comment: »The absence of any wren of the *aedon* type as a breeding bird in temperate Mexico is due either to lack of field work at the proper season, or perhaps to unfavorable competition there with a related species, *T. brunneicollis*.» Wetmore (1957) considered *musculus* conspecific with *aedon* but did not comment on *brunneicollis*. Paynter (1957) was the first to suggest using *brunneicollis* as the connecting link between *aedon* and *musculus*, but admitted there is currently no evidence of either intergradation or sympatry between *brunneicollis* and *musculus*. An understanding of the biological relationship of *aedon* (now including *brunneicollis*) and *musculus* must await further study in the poorly worked region of southern Mexico, to see whether *brunneicollis* there grades into *musculus* as it does into *aedon* in the north.

Summary

A reexamination of the House Wren populations along the United States — Mexico border has furnished evidence for considering the Brown-throated Wren of Mexico, *Troglodytes brunneicollis*, conspecific with the House Wren of North America, *Troglodytes aedon*. A cline of morphological characters between the two forms

[1] The population of central northern United States, sometimes called *T. a. baldwini*, has recently been synonymized with the nominate race (Paynter 1957).

has been demonstrated, though the gradient is steep due to restricted gene flow. There is no significant difference in their breeding behavior, nests, or eggs. Sound spectrographic analyses of vocalizations indicated greater similarity between Mexican and North American populations than between the two races of the North American form. The »lumping» of *aedon* and *brunneicollis* may help to clarify the relationship of *aedon* with *musculus* of Central and South America, but further field work is needed on this point.

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The Primeval Immigration of some Forest and Open-Land Birds into Denmark

Bernt Løppenthin

Denmark

Without the activity of man Denmark would doubtlessly have been totally covered by deciduous forest, only broken by the inner seas; but if we set aside the proportionally very small areas of deciduous woods and conifer plantations the land to day is completely open. In recent time forest birds amount much less in Denmark than birds of the open land, either of arable land, coastal meadows or heaths etc.

When the ice cap of the Würm Glaciation had withdrawn from Denmark some 15000 years ago the natural appearance of the country was quite arctic. In the following millennia smaller ameliorations of the climate are noticed, but not till about 8000 years B.C. the conditions were so favourable that the coniferous forest was able to thrive. In the beginning the dominant trees were Birch and Pine. Later, about 7000 years B.C., the Pine was prevailing, and there invaded an undergrowth of Hazel. Some 1000 or 1500 years later the Lime immigrated. At the time mentioned here Denmark was part of the Northwest European Continent. The coastal line extended from Great Britain to some place north of the present Jutland, which was separated from Norway by a sound; this proceeded into a fjord along the coast of Sweden to the northern part of Scania and Sealand, which were in land-connection with each other. During the Pine-hazel Period, the Boreal Period, lasting from about 7000 to about 5000 B.C., Denmark was inhabited by mesolithic people, who have left evidence of some 25 species of birds (Winge, 1903 and 1925). Of these only one, a single specimen of *Tringa totanus*, was a true open land bird; of the rest about $^3/_5$ were water birds, and $^2/_5$ were true forest birds or arboreal birds with some affinity to water.

In the centuries around 5000 B.C. the sea rose to a somewhat higher level than to-day, and the inner Danish seas as well as the Danish Islands were formed. The huge Baltic lake became openly connected with the sea through the Belts and the Sound. The temperature had risen, and the Pine gave way, as the dominant tree of the forest, to the Oak and the Elm. In this period, the Atlantic Period, lasting to about 2500 B.C., the human inhabitants were hunters, and they ate many birds. In the kitchen-middens of their dwellings near the coasts they have left evidence of

some 50 species of birds, of which only one, a single specimen of *Philomachus pugnax*, was a true open land bird. Of the rest some $^3/_5$ were aquatic species and $^2/_5$ genuine forest birds or arboreal species with some affinity to water; *i. e.* the proportions were much the same as in the deposits from the Boreal Period.

Other finds have indicated that the whole country was forest clad; and estimating from the fairly rich material of fossil birds' bones from Denmark of this period it is most probable that the human inhabitants obtained their prey in a country of that type. The population was stone-age people without knowledge of agriculture and without domestic animals apart from dogs. As it is to be expected few marine birds were taken during the Boreal Period and only such that occasionally occur in fresh water. During the Atlantic Period lots of marine birds were caught; but apart from the two single specimens of Waders no bird of the flat, open land is represented in the whole material. This type of landscape, which to-day is widely distributed in Denmark, certainly did not exist before agriculture began.

When I was studying Danish breeding birds and their immigration, my attention was drawn to the absence of statements from the material of the kitchen-middens of three species of birds, which very often are claimed to be forest or wood-land species, viz. *Ciconia ciconia*, *Lyrurus tetrix* and *Corvus corax*. There is no obvious reason to imagine that the Danish stone-age-dwellers should have avoided these birds from some kind of superstitious feeling. They caught everything which they could get from *Grus grus*, *Haliaeetus albicilla* and *Pinguinus impennis* down to *Podiceps ruficollis* and *Phoenicurus phoenicurus*.

Ornithologists with the most comprehensive knowledge of the life of the Storks as Siewert (1932, p. 123—127) and Lange (1942, p. 75) have expressed the opinion that the original breeding haunt of *Ciconia ciconia* was moist open forest. I consider this to be true of *Ciconia nigra*; but *Ciconia ciconia* I regard as a bird of steppe or savannah country. Fossil bones of *Lyrurus tetrix* and *Corvus corax* have now and then (*e. g.* Koken, 1912, p. 187) been used to support suppositions of the occurrence of more extensive forest, but both are certainly true open land birds. Neither of them avoid woods, near the margin of which they may place their nests, but they display in the open, and they mostly feed in the open.

Bones of *Ciconia nigra*, which are a little smaller than those of *Ciconia ciconia*, are known from Denmark from both Boreal and Atlantic Periods. There are not many specimens, but most likely the stone-age-hunters were not able to exploit this species too much on account of its solitary habits deep in the extensive forest. As to *Ciconia ciconia*, no fossil find has been identified at all from Denmark. This species was simply not able to live in this country till the forest was cleared away to an extensive degree. In the Subboreal Period, which began about 2500 years B.C., the people of the New Stone-age began to burn the forest to establish a primitive agriculture; but this was certainly not enough to attract *Ciconia ciconia*. The clearings made by the first Danish farmers were not permanent. When the soil was exhausted, they moved to other places, where the forest had been burned, and after

a series of years the abandoned fields were covered with forest again. In the beginning of the Subatlantic Period, from about 500 years B.C., the iron-age-peasants with their much better tools were more able to suppress the forest. Compared to the preceding period the climate grew cooler and moister, and the cattle and other domestic animals were taken into stables during the winter. I do not believe, however, that *Ciconia ciconia* immigrated so early. Odin, the head of the Norse gods of that time, had two Ravens sitting on his shoulders; they told him all the news collected throughout the world. Swans and an Eagle were also present in the vicinity of the Norse gods, but no Storks. The houses of the iron-age peasants were probably big enough to support a stork's nest; but most likely there were none. If *Ciconia ciconia*, the White Stork, had played any part whatever in the lives of the iron-age inhabitants of Denmark, there might be a possibility of a record of a stork's nest from the roof of Gladsheim, the castle of Odin. In the medieval popular ditties, with Danish text, Storks are also completely lacking.

Regarding the Danish place-names there are certainly some, about fifteen, which are named after Storks; of these one third undoubtedly origin from *Ciconia nigra*, the Black Stork, and one third from the White Stork, while the remaining third may have been named from either of these two species. Certainly the names were given at most different times; but nevertheless it is obvious that Storks played a very little part if any in the range of idea of man, when the oldest place-names of Denmark were given. Probably no Danish place-name with Stork is older than some hundreds of years. A comparison with other place-names in Denmark, which are given after birds, shows that there are twice as many names with Swan as names with Stork, three times as many names with Crane, nine times as many names with Crow and eleven times as many names with Raven. A couple of place-names with these birds are per haps at least 1500 years old, and there are many, which are 900—1000 years old (cf· Steensberg, 1942, p. 43—44).

About the 12th century the exploitation of the Danish woods was intensified very much, and this went on till the 18th century, when only wretched wood-ruins were left. All over the country moist commons gave feeding conditions eminently suitable for a numerous population of White Storks, which often bred in colonies. I should believe that *Ciconia ciconia* immigrated into Denmark at 1200—1300 A.D., not earlier. During the following centuries it was numerous; but this period was a time of economic stagnation for agriculture in Denmark. The peasants were bound to the soil and lived close together in their villages, which were separated by proportionally extensive uninhabited areas. From late in the 18th century many important agricultural reforms were carried out by various commissions; especially worth mentioning is the emancipation of the villenage in 1788. The old community farming was by and by given up; the soil was allotted, and the farm buildings were spread over the countryside. The agricultural methods were improved, the soil was extensively drained, and the vast, swampy commons were brought into cultivation. This was good for the increasing human population, but not for the White Storks. The people

loved these birds; they returned every spring to the peasant's roof, and were treated as »sacred birds» of Denmark. But in the long run wheels on the top of the barns do not attract the White Storks looking for nesting places, when other life conditions, especially those of foraging, have been reduced. From the middle of the 20th century it was evident that the breeding population of *Ciconia ciconia* in Denmark was decreasing. It was, it is true, still numerous about the turn of the century, and the nests were widespread over the country. In the 1930ies the population was estimated at about 1000 pairs (LANGE, 1942, p. 86). To-day there are left hardly 200 pairs, practically all of which occur in swampy districts in Jutland.

Ciconia nigra probably has stopped breeding in Denmark; the last nesting on record was in 1951. Concerning *Ciconia ciconia* I should not be too surprised if it had ceased to breed in Denmark at the turn of the next century. If it is exterminated, it will be by the effects of tractors and excavators.

Fossil bones of *Tetrao urogallus* give evidence that this species lived in Denmark in both Boreal, Atlantic and Subboreal times (LØPPENTHIN, 1955); it was certainly eaten by the stone-age-people for about 5000 years. It is generally supposed that *Tetrao urogallus* died out in Denmark in prehistoric times, *i. e.* before 1000 A.D.; but perhaps it survived for some centuries more. At any rate there are reports that this species still survived in the extensive woods in South Jutland in the 18th century, but definite evidence of this is lacking. I believe that *Tetrao urogallus* had actually disappeared from Danish soil at that time, but not much earlier.

Regarding the fairly considerable material of remains of *Tetrao urogallus*, the Capercaillie, from the Danish kitchen-middens, it is worth mentioning that *Lyrurus tetrix*, the Black Grouse, is totally absent from this material. It is of no sense at all to suggest that the stone-age-hunters caught and ate the Capercaillies but let the Black Grouse fly again, if they had been able to trap them in any way. It is true that a single bone of *Lyrurus tetrix*, found in a peat-bog near Copenhagen, is on record (WINGE, 1903, p. 89); but there are objections to this specimen. It is »from the unknown past»; *i. e.* it is not from an ancient cultural layer, and it has not been possible to identify the bone as belonging to any definite climatic period. The determination of the bone as *Lyrurus tetrix* was done by HERLUF WINGE and seems indisputable. It is a tibiotarsus of which the lower end is lacking, *i. e.* just the part of that bone, which in recent time is left in a bird, when it is roasted. I suppose that this bone is refuse from a human meal in the very recent past, when lots of Black Grouse were imported from other Scandinavian countries and sold for food in Copenhagen. I do not believe that *Lyrurus tetrix* has lived in Denmark during the time that the land was totally covered with forest, *i. e.* from about 8000 B.C. till the farming people of Antiquity had been active for some centuries. *Lyrurus tetrix* roost readily in trees, but the leks are in the open country. It certainly had no chance to make its way into Denmark before 2000—1000 years B.C., when the primitive agriculturists had burned the forest to some degree; but most likely the immigration did not take place till two or three thousands of years later, *i. e.* when the heaths of Jutland were

fully developed (cf. JONASSEN, 1950). I suppose that the present population of *Lyrurus tetrix* in Jutland originates from birds, which immigrated from the south about 1100 to 1300 A.D. This species has never come spontaneously to the Danish Islands with their clayey soil, where the Heather has never covered so extensive an area as in Jutland.

From the Boreal Period of Denmark we know of Corvine birds only *Garrulus glandarius*, the most pronounced forest inhabitant of the species in question. In the Atlantic Period, when most of the sea-coasts were formed, *Corvus cornix* was able to thrive, and the bones of this species has been found in a good many places. *Corvus corax* and *Coloeus monedula* are not represented in the material from the forest period, but both are known from cultural finds of the Bronze Age, *i. e.* from the late Subboreal Period, about 1000 years B.C. *Corvus corax* and *Coloeus monedula* roost and nest freely in trees; but they are open land feeders for which no life conditions were present in Denmark till the forest had been cleared away to some degree.

By the facts and supposition I have mentioned, I would point out the danger of placing a species of bird in a landscape community, which does not correspond to *all* factors of life conditions of the species concerned. *Ciconia nigra, Tetrao urogallus* and *Garrulus glandarius* are true forest species, and they are known from Denmark from the period, when the country was totally covered by forest. All are known from the Boreal Period, and the former two also from the Atlantic Period. *Ciconia ciconia, Lyrurus tetrix, Corvus corax* and *Coloeus monedula* are not known from Danish deposits of the forest period. They feed and display in the open, and they must be considered open land birds notwithstanding their partiality to trees.

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On the Biological Races of the Common Cuckoo, *Cuculus canorus* L. in the Territory of the European part of the USSR

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The character of the biological relations between the cuckoo (*Cuculus canorus* L.) and its hosts, the passerine birds, is far from being clear for the whole range of this parasite. The regions of the European part of the USSR have been comparatively little studied in this respect.

Pursuing his object of finding out the list of species which foster the cuckoo's young in the territory of the European part of the USSR, the author has added to the existing data in the literature, and to his own observations, not yet published, the information obtained from a number of ornithologists, who have kindly sent him their notes from different regions of the country. For this information the author is sincerely thankful to E. V. Kumari (Tartu), K. A. Vilks (Strenchi), G. A. Michelson (Riga), N. J. Gavrilenko (Poltava), U. M. Zubarovski (Kijev), E. P. Spangenberg (Moscow), E. V. Lukina (Leningrad), and also to A. S. Lisetski (Charkov), A. N. Formozov (Moscow), S. V. Kirikov (Moscow), T. L. Ivanauskas (Kaunas), K. N. Blagosklonov (Moscow), N. P. Kadochnikov (Leningrad), I. A. Isakov (Moscow), A. G. Bannikov (Moscow), V. N. Charlemagne (Kijev), A. P. Kusjakin (Moscow), S. N. Varshavski (Aralsk), N. N. Danilov (Sverdlovsk), P. S. Kozlov (Volsk), S. M. Semjenov (Voronjezh), D. P. Bogatjrev (Bichek) and to many other Sovjet ornithologists.

Thus, in all, 477 records of the eggs and young of the common cuckoo have been noted in the nests of 48 species of our singing birds. Out of this number there are 12 species in which fostering of the cuckoo is not yet established: only eggs of the common cuckoo were found in their nests. These cases are marked in the enclosed list by an asterisk. (See Table 1.)

The majority of the singing birds of the 36 species in whose nests, on the territory of the USSR, the young of the common cuckoo had been found, should be put into the group of accidental, or secondary, hosts. Though many of them are well-known and common birds, still the cuckoo's eggs and young had been found in their nests only once or a few times. On the territory under study such are: *Passer montanus*, *Emberiza citrinella*, *Alauda arvensis*, *Motacilla flava*, *Anthus campestris*, *Lanius minor*,

Phylloscopus sibilatrix, Hippolais icterina, Sylvia nisoria, Sylvia atricapilla, Turdus musicus, Delichon urbica and also *Luscinia svecica, Fringilla montifringilla, Carduelis flammea* and *Carduelis spinus.*

The siskin, *Carduelis spinus*, has not yet been accorded as the host of the common cuckoo at all. A young cuckoo being fed by a pair of siskins was observed by J. A. Neifeldt in Karelia (verbal communication).

The Brambling *(Fringilla montifringilla)* in the northern part of Finland, according to the information of Wasenius (1926), fosters young cuckoos often enough. There exists a special group of cuckoos which lay eggs of »*Fringilla* type». Most probably, the same biological group of cuckoos, or one very near to it, is spread in the north-western part of the USSR, where it parasitizes, mainly, Chaffinches *(Fringilla coelebs)* whose eggs are similar to those of the Brambling. The cuckoos laying eggs of the *Fringilla*-type have also been recorded in central regions of the European part of the USSR. But they are here less numerous and have apparently lost their connection with their primary host. Cuckoo's eggs of the *Fringilla*-type were found, for instance, in the Moscow district, in the nests of *Erithacus rubecula, Phylloscopus collybitus, Phylloscopus sibilatrix* and in no single case in the nests of *Fringilla* itself. In general, the number of cuckoos laying eggs of the *Fringilla*-type is evidently not high. On the territory of the European part of the USSR this race, in contrast with some others, cannot be called a flourishing one. The cuckoos parasitizing *Phylloscopus trochilus* are also not numerous, and their range is limited to the north-western regions of the USSR.

The secondary hosts of the common cuckoo in the limits of the territory under study are also *Lanius collurio* and all species of *Sylvia*. In the nests of these birds in the USSR the eggs and young of the common cuckoo have been found comparatively seldom. The cuckoo's eggs discovered in the clutches of *Lanius collurio* and of *Sylvia* spp. often differ very strongly from those of the nest-owners, and besides they are only rarely accepted, which shows that in the majority of regions of the European part of the USSR the biological relations between the cuckoo and the above-mentioned species are not yet well established and sometimes simply accidental.

Of interest is the fact that *Lanius collurio*, as well as different species of *Sylvia*, in Germany are acknowledged as the primary hosts of cuckoos (R. Stimming, 1927; W. Makatsch, 1955). In all probability, the representatives of this biological race of cuckoos concentrate somewhere in the western parts of Europe. Approximately the same characteristic range is typical for some other groups of cuckoos, parasitizing, for instance, *Anthus pratensis, Anthus trivialis, Motacilla flava* and *Troglodytes troglodytes*. In many regions of Western Europe these species rank as primary hosts (W. Makatsch, 1955), but in the USSR they are secondary or accidental hosts of the common cuckoo. On the contrary, *Muscicapa striata, Acrocephalus arundinaceus, Phoenicurus phoenicurus, Saxicola rubetra* and also *Turdus ericetorum, Hirundo rustica*, and some other birds of the USSR apparently much more often bring up the cuckoo's young than in Western Europe.

Muscicapa striata is one of the commonest hosts of cuckoos in Baltic republics and such is *Acrocephalus arundinaceus* in southern parts of the European Russia.

Cuckoos laying eggs into the nests of *Turdus ericetorum* are not numerous. A few have been recorded in the Baltic (H. LOUDON, 1895), in the Voronjezh-district (BARABASH-NIKIFOROV and PAVLOVSKY, 1948) and also in the environs of Moscow and in the Ukraine.

The eggs of these cuckoos, according to verbal communication of A. G. BANNIKOV, in Moscow district, are of a clear, light-blue colour. Apparently, the initial or primary host of this group of cuckoos is *Phoenicurus phoenicurus*. Still, it would be yet too early to speak about an independently existing cuckoo's race parasitizing *Turdus ericetorum*.

Also not yet clear is the extent of independence of cuckoos parasitizing *Hirundo rustica*. The colour of eggs layed by these cuckoos in the USSR has not yet been ascertained. *Hirundo rustica* is perhaps a secondary host of the biological group of cuckoos connected with *Motacilla alba*. Details of the findings of the young of the cuckoo in the nests of *Hirundo rustica* have been recorded from Estonia (P. WASMUTH, 1909), Ukraine (GAVRILENKO) and the Voronjezh-district (BOGATJREV). The colour of eggs layed by cuckoos in the nests of *Passer montanus* is not known either (PORTENKO, 1928). It is not unlikely that these eggs are also of the *Motacilla*-type.

One of the most flourishing races of the common cuckoo on the territory of the European part of the USSR is the race laying clear light-blue eggs. Its principal hosts

Photo 1. A three week young cuckoo and the female of *Phoenicurus phoenicurus*. The young cuckoo has just come out of the nest made inside a rotten stump. Voronjezh district, the 5th of July, 1951. Photo: A. S. MALCHEVSKY.

Photo 2. A young cuckoo brought up in one nest with the young of *Phoenicurus phoenicurus* Voronjezh district, the 18th of June, 1952, Photo: A. S. Malchevsky.

are *Phoenicurus phoenicurus* (photo 1) and *Saxicola rubetra*. One of these species must apparently be the primary host, while the connection with the other must have arisen somewhat later. It is difficult to suppose that one and the same cuckoo might at one time parasitize both species.

The attachment of cuckoos to a certain host is well known. It is maintained from generation to generation, evidently by their nestling-habits (Promptov, 1941). At the same time it is doubtful that the light-blue colouration could arise in both groups of cuckoos independently, during the period of interrelations between the parasite and each of the above-mentioned species. It is more likely to suppose one of them to be the most ancient host. The history of relations with it had led to the formation of a special population of cuckoos, laying light-blue eggs. Such adaptation might have given to the cuckoos of this group the possibility of widening the sphere and of passing on to another species having light-blue eggs. After that, the original race might have divided into two groups of cuckoos, differing in their habits, but having, in general, a common hereditary basis, which manifests itself, in particular, in laying similarly coloured eggs.

Apart from the light-blue colouring of the egg-shell, it should be pointed out that the cuckoos parasitizing *Phoenicurus phoenicurus* inhabit pine forests or mixed pine and birch forests and that sometimes, a young cuckoo is reared together with the young of *Phoenicurus phoenicurus* (photo 2). Besides that, as our experiments show (Malchevsky, 1954; Kadochnikov, 1956), the cuckoos

of this race lay eggs always sitting in the nest of its owner, but not carrying them in their bill.

The author has not succeeded in establishing that these cuckoos destroy the nests of *Phoenicurus phoenicurus*, a habit often estimated as an adaptive form of the parasite's behaviour. Thus, even if such acts as the destroying of brooded clutches take place, they are not typical for all the cuckoos.

The cuckoos laying light-blue eggs form evidently a well-isolated race. They are often met with in the districts inhabited by cuckoos of another origin, which lay eggs, for instance, of the *Acrocephalus*-type. So, according to our observations in the Voronjezh-district (MALCHEVSKY, 1954) during the period of reproduction, the cuckoos laying eggs of the *Phoenicurus*-type, as well as of the *Acrocephalus*-type, concentrate in spring in the neighbourhood of the nests of the appropriate species, which differ in their ecology. This results in ecological separation of both races: the cuckoos with eggs of the *Phoenicurus*-type inhabit, as has been said, the pine forests, while those having eggs of the *Acrocephalus*-type concentrate in flood-lands.

The cuckoos laying light-blue eggs and parasitizing *Phoenicurus phoenicurus* are widely spread in the USSR. They have been recorded in almost all districts of the European part of the USSR. As is known, in Finland they are met even more often than the cuckoos associated in their reproduction with *Motacilla alba* (E. WASENIUS, 1926). Westwards, the number of these cuckoos becomes considerably less. In England they are almost completely absent. (WITHERBY and others, 1952.)

One of the most widely spread in the USSR is the *Motacilla alba* type. According to the number of findings of its eggs and young in the nests of our passerine birds, it takes the first place (113 cases out of 477 known). Cuckoo's nestlings being reared by *Motacilla alba* were observed almost all over the territory of the USSR. The cuckoo's eggs found in these nests are usually of mimicry type. This shows that biological relations between the cuckoo and its hosts depend on historical reasons and that they are consolidated by natural selection.

Of a somewhat peculiar character are the relations between the cuckoo and *Erithacus rubecula*, which in the USSR is one of the usual and widely spread cuckoo's hosts. The fact is that the cuckoo's eggs found in the nests of *Erithacus rubecula* show a strong variety in the colouration of their shell. In the majority of cases they are similar to the eggs of different birds also known as hosts of cuckoos, as, for example, *Phoenicurus phoenicurus*, *Fringilla coelebs*, *Motacilla alba*. But these eggs are never like the eggs of *Erithacus rubecula* itself. Thus, admitting into its nest the eggs of different cuckoos, *Erithacus rubecula* systematically brings up young cuckoos of different origins. This may result in practical mixing of cuckoos, the offsprings of different biological groups concentrating in spring in the neighbourhood of the nests of *Erithacus rubecula*. It is difficult to say to what extent such mixing of races may affect the colouration of the egg-shell of the »hybrid» origin, because up to now we do not know anything for certain about the inner character of inheriting this indication within the cuckoos. It is possible that cuckoo's eggs of

mixed or intermediate type just appear as the result of mixing of different biological groups of cuckoos. It is equally possible to suppose that natural selection, working with this material later on, may lead to the establishment of close connections between the common cuckoo and some new species.

TABLE 1

Birds in whose nests on the territory of the European part of the USSR the eggs or young of Cuculus canorus canorus L. were found. Number of records.

Hosts	Baltic	Bielorussia	Ukraine	Northwest of the European part of the USSR	Northeast of the European part of the USSR	Central forest regions of the European part of the USSR	Central forest-steppe regions of the European part of the USSR	The Middle and South Volga	The Middle and South Ural	The South of the European part of the USSR and the Caucasus	Total: eggs and young
1 Sturnus vulgaris *	1	—	1	—	—	—	—	—	—	—	2
2 Chloris chloris *	3	—	—	—	—	—	—	—	—	—	3
3 Carduelis spinus	—	—	—	1	—	—	—	—	—	—	1
4 C. cannabina *	2	—	—	—	—	—	—	—	—	—	2
5 C. flammea	—	—	—	—	1	—	—	—	—	—	1
6 Pyrrhula pyrrhula *	—	—	—	—	—	—	—	—	1	—	1
7 Erythrina erythrina *	—	—	—	1	—	—	—	—	—	—	1
8 Fringilla coelebs	4	—	—	5	—	—	—	—	—	—	9
9 F. montifringilla	—	—	—	1	—	—	—	—	—	—	1
10 Passer monitanus	—	—	1	—	—	—	—	—	—	1	2
11 Emberiza citrinella	3	—	—	—	—	—	1	—	—	—	4
12 Alauda arvensis	1	—	—	—	—	—	1	—	—	—	2
13 Motacilla alba	48	4	13	4	2	7	15	10	5	5	113
14 M. flava	—	—	—	—	—	2	—	—	—	—	2
15 Anthus pratensis *	2	—	—	—	—	—	—	—	—	—	3
16 A. campestris	—	—	—	—	—	—	1	—	1	—	2
17 A. trivialis	3	—	5	—	—	—	1	1	—	2	11
18 A. spinoletta	—	—	—	—	—	—	—	—	—	1	1
19 Lanius collurio	3	—	5	—	—	—	1	1	—	2	12
20 L. minor	—	—	—	—	—	—	1	—	—	—	1
21 Muscicapa striata	21	1	3	—	—	2	2	—	—	1	30
22 M. hypoleuca *	2	—	—	—	—	—	—	—	—	—	2
23 Phylloscopus collybitus	4	—	1	—	—	1	—	—	1	—	7
24 Ph. trochilus	3	—	—	6	—	—	—	—	—	—	9
25 Ph. sibilatrix	1	—	—	—	—	2	—	—	—	—	3
26 Acrocephalus palustris	—	—	3	—	—	—	5	1	—	—	9
27 A. arundinaceus	—	—	24	—	—	—	1	5	—	2	32
28 A. agricola	—	—	1	—	—	—	—	—	—	—	1
29 Cettia cetti	—	—	—	—	—	—	—	—	—	2	2
30 Hippolais icterina	4	—	—	—	—	—	—	—	—	—	4
31 Sylvia nisoria	1	—	2	—	—	—	—	—	—	—	3
32 S. communis	1	—	5	—	—	—	3	—	—	2	11

* Species in the nests of which only eggs were found.

TABLE 1

Continuation

Hosts	Baltic	Bielorussia	Ukraine	Northwest of the European part of the USSR	Northeast of the European part of the USSR	Central forest regions of the European part of the USSR	Central forest-steppe regions of the European part of the USSR	The Middle and South Volga	The Middle and South Ural	The South of the European part of the USSR and the Caucasus	Total: eggs and young
33 S. curruca	2	—	2	—	1	—	3	1	—	—	9
34 S. borin	3	—	7	—	—	—	2	—	—	—	12
35 S. atricapilla	—	—	2	1	—	2	—	—	—	—	5
36 Turdus pilaris *	2	—	—	—	—	—	—	—	—	—	2
37 T. musicus	3	—	—	—	—	—	—	—	—	—	3
38 T. ericetorum	1	—	6	—	—	1	2	—	—	—	10
39 T. viscivorus *	1	—	—	—	—	—	—	—	—	—	1
40 T. merula *	—	—	—	—	—	—	1	—	—	—	1
41 Erithacus rubecula	5	—	6	13	—	10	1	—	—	—	35
42 Phoenicurus phoenicurus	26	1	9	7	—	—	31	1	3	—	78
43 Saxicola rubetra	9	—	2	6	—	2	1	—	—	1	21
44 Luscinia svecica	—	—	1	—	—	—	—	—	—	—	1
45 Prunella modularis *	—	—	—	—	—	—	1	—	—	1	2
46 Troglodytes troglodytes *	1	—	—	—	—	—	—	—	—	—	1
47 Hirundo rustica	2	—	1	—	—	—	5	—	—	—	8
48 Delichon urbica	—	—	1	—	—	—	—	—	—	—	1
Totals:	162	6	97	45	4	32	79	19	14	19	477

* Species in the nests of which only eggs were found.

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Zur Siedlungsdichte des Roten Milans *(Milvus milvus* (L.)), seinem Schaden an Hausgeflügel und seiner Abwehr

(vorläufige Mitteilung)

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Der Rote Milan, im Flugbild einer unserer schönsten Greifvögel, ist in Deutschland grösstenteils selten. Manchen Gegenden fehlt er seit Jahrzehnten sogar ganz, u. a. weiten Gebieten Schleswig-Holsteins, Sachsens und Ostthürigens. Nordwestthüringen hatte in den letzten 30 Jahren einen guten Bestand an Roten Milanen, die in den Höhenzügen, wie Hainich, Hainleite, Finne, aber auch gelegentlich in kleinen Feldgehölzen brüten. In der Flur Seebach bei Mühlhausen in Thüringen kann man täglich 1—2 Milane sehen, im Frühjahr und Herbst zur Zugzeit auch gleichzeitig 10—15, zumal wenn sie an günstigen Hanglagen im Aufwind ihre Flugspiele ausführen.

Ähnlich war die Siedlungsdichte auch im nördlichen Harzvorland, wo es z. B. im Hohen Holz, einem etwa 1,400 ha grossen Laubmischwald auf einer Höhe bei Oschersleben an der Bode südlich Halberstadt 2—3 Paar Rote und 3—4 Paar Schwarze Milane (*Milvus migrans* (Boddaert)) gab. Um 1942 und stärker ab 1945, vielleicht mit veranlasst durch das Fehlen von Schusswaffen, begann in fast allen Milangebieten ein Anstieg der Brutpaare. Im Hohen Holz wurden bei einer ersten Zählung durch die Forstangestellten H. Klimke und G. Stachowiak 1955 gegen 40 Brutpaare gezählt. Aufgrund der zahlreichen Klagen über erhebliche Hühnerverluste durch die Milane gab die Zentrale Naturschutzverwaltung 1956 eine beschränkte Abschussgenehmigung. 10 Altvögel wurden als erlegt gemeldet, wahrscheinlich waren es jedoch mehr. Eine erneute Zählung ergab für 1957 nur noch 27 besetzte Horste. Davon wurden 2 Brutpaare abgeschossen, 3 weitere Bruten von Menschenhand vernichtet. 1958 stellten wir bei einer Zählung Mitte Mai mit Untersuchung jedes einzelnen Horstes mindestens 45 Brutpaare des Roten Milans fest. Die Horste standen im 20—30 m hohen Altholz, meist Buchen, gelegentlich Eichen, Kiefern und Lärchen. Auf einzelnen bevorzugten Flächen am Feldrand standen die

Horste kolonieartig zusammen, wie es im vorigen Jahrhundert in Deutschland öfter beobachtet wurde. Es brüteten z. B. im »Neindorfer Hagen» 5 Paare auf 16 ha und im »Brand» 4 Paare auf 5 ha.

Der Schwarze Milan vermehrte sich seit 1945 nicht, sondern ging auf meist 2—3 Paare zurück. Mäusebussarde (*Buteo buteo* (L.)) wurden alljährlich mit 8—11 Paaren festgestellt, dazu 2—5 Paar Habichte (*Accipiter gentilis* (L.)), meist auch je ein Paar Wanderfalken (*Falco peregrinus* L.) und Baumfalke (*Falco subbuteo* L.). Eine ähnliche Brutdichte von Roten Milanen haben der Huy und der Hakel, weitere Höhenzüge im nördlichen Harzvorland, aufzuweisen.

Dies gehäufte Auftreten des Milans wird begünstigt durch den Bestand an älterem Baumholz, in erster Linie aber wohl durch die in den weiten Feldern der fruchtbaren Magdeburger Börde oft in Überfluss vorhandenen Mäuse, vor allem Feldmäuse (*Microtus arvalis* (Pallas)) und Hamster (*Cricetus cricetus* L.). In einzelnen Jahren mit Mangel an diesen Nagern mögen die Milane besonders zur Zeit der Jungenaufzucht Kücken des Haushuhnes (*Gallus domesticus* autor.) geraubt haben. Nach Gewöhnung an diese bequeme Beute wurde von manchen Milanen der Geflügelraub auch in normalen Jahren fortgesetzt, zumal wenn die Nager im Mai und Juni gute Deckung in den hochwachsenden Feldkulturen fanden. Der Schaden hörte stets auf, sobald immer mehr Felder abgeerntet wurden und damit die Nager leichter erreichbar waren.

Einige Milane wurden zu Spezialisten, die auch öfter erwachsene Hühner schlugen, zum Teil ihre Raubflüge bis mitten in die Dörfer ausdehnten und die Kücken ohne Scheu sogar unmittelbar von den Höfen holten. Im allgemeinen wurden aber die am Dorfrand nach dem Walde zu gelegenen Gehöfte bzw. Hühnerausläufe am stärksten heimgesucht. Verluste von durchschnittlich 10—15 Junghühnern je Geflügelhaltung, vereinzelt bis 100 Tiere auf grösseren Ausläufen, waren in den betroffenen Dörfern keine Seltenheit.

Zweifellos waren an diesen Schäden auch Habichte beteiligt, den Hauptanteil verursachten jedoch die Milane. Zahlreiche geschlagene Hühner konnten wir in unseren mehrjährigen Beobachtungen einwandfrei als Milanbeute erkennen. Während nämlich der Habicht schon durch den Griff der langen scharfen Krallen sein Opfer tötet, ist der Milan mit seinen kurzen Krallen dazu nicht in der Lage. Er stürzt sich vielmehr auf das Huhn, versucht es festzuhalten und durch kräftige Schnabelhiebe auf den Kopf zu töten. Die starken blutigen Kopfverletzungen sind daher ein sicherer Hinweis für den Milan.

Scheuchmittel, glänzende oder farblich auffallende Gegenstände, die gegen den Habicht zeitweise wirksam sind, versagten gegen den Milan schnell. Er kreist lange über dem Hühnerauslauf oder sitzt in der Nähe aufgeblockt und erkennt nach wenigen Tagen die Ungefährlichkeit der Scheuchen.

Perlhühner (*Numida meleagris* (L.)) blieben mit ihrem Geschrei bald unbeachtet, eins wurde sogar geschlagen. Truthühner (*Meleagris gallopavo* L.) wirkten mitunter als guter Schutz. Mit der Zeit wussten sich jedoch die Milane anzupassen und schlu-

gen die Hühner im jeweils entfernteren Teil des Auslaufes. Von einem besonders hartnäckigen Spezialisten wurden in Beckendorf, Kreis Oschersleben, sogar täglich Kücken geschlagen, die ein Truthahn in unmittelbarer Nähe des Wohnhauses führte. Nach Abschuss des Räubers hörte der Schaden auf. Als Warner taten jedoch Truthühner gute Dienste, da sie schon bei Annäherung der Greifvögel von weitem warnten und die Hühner es bald lernten, bei diesem Zeichen in Deckung zu gehen. Hausgänse (domestizierte *Anser anser* (L.)) mit Jungen erfüllten den gleichen Zweck.

Am besten bewährte sich ein lebhafter Hund *(Canis familiaris)* mittlerer Grösse, etwa ein Terrier oder Spitz. Dieser wird darauf abgerichtet, jeden anfliegenden oder kreisenden Raubvogel anzubellen. In mehreren Fällen bei Oschersleben und in Thüringen waren damit bereits gute Erfolge zu verzeichnen.

Als sehr wertvoll erwiesen sich Schutzvorrichtungen, in denen die Hühner bei Annäherung der Greifvögel Zuflucht und Deckung finden. Es eignen sich dafür niedrige Buschgruppen, am besten mit bis zum Boden überhängenden Zweigen. Wir verwenden gern die Alpenjohannisbeere *(Ribes alpinum)*, je 3 Sträucher in einem Meter Abstand zusammengepflanzt. Es genügen auch kleine Schutzgerüste von 40 cm Höhe aus Stangen, die mit Brettern, Dachpappe oder Reisig zum Teil auch nach den Seiten herunter abgedeckt werden. Besonders abgelegene Auslaufflächen sollten mit solchen Deckungsmöglichkeiten versehen sein. Obstbäume sind dagegen eine gewisse Gefahr, da die Milane dann leicht ungesehen herankommen und plötzlich herunterstossen. Aus diesem Grunde sollten Geflügelausläufe möglichst im freien Gelände liegen, das einen guten Weitblick gestattet und mit ausreichenden niedrigen Zufluchtsstellen versehen ist.

Bei einzelnen hartnäckigen Spezialisten lässt sich ihre Beseitigung nicht umgehen. Der Fang gelingt meist nicht mit den üblichen offen aufgestellten Habichtskörben und Habichtsfängen, da der Milan offenbar vor dem Drahtgitter zurückschreckt. Wir beabsichtigen Versuche mit dem Oberteil eines Habichtskorbes als Bodennetz, gut getarnt mit Sand oder Häcksel. Der Durchmesser der Netzbügel muss jedoch wenigstens 90 cm betragen, da sonst Verletzungen der Flügel vorkommen. Tellereisen sollten selbstverständlich wegen der damit verbundenen Quälerei unbedingt verboten werden. Man könnte auch eine Verpflanzung von Milanen aus Gebieten grosser Siedlungsdichte in Gegenden, wo sie fehlen, versuchen. Dabei ist es allerdings noch ungeklärt, wie weit die Vögel in ihr altes Revier zurückgehen.

Der Abschuss sollte stets nur als letzte Lösung gewählt werden, denn es ergeben sich dabei durch Unkenntnis oder Gleichgültigkeit der Jagdberechtigten oft Verluste an anderen geschützten Greifvogelarten. Deshalb dürften dazu nur ornithologisch besonders erfahrene Jäger ausgewählt werden.

Leider häufen sich die Meldungen von Übergriffen einzeln brütender Paare aus den verschiedensten Gegenden. Um diese nicht beseitigen zu müssen, sollten in erster Linie die vorbeugenden Schutzmassnahmen empfohlen werden. Dass solche Übergriffe von einzelnen Milanpaaren vorkommen, haben wir selbst seit Jahrzehnten an den Geflügelfarmen am Rande des Dorfes Seebach festgestellt. Verschiedentlich

sind damals die Spezialisten abgeschossen worden. Seit etwa 9 Jahren blieben jedoch die beiden Farmen von Geflügelverlusten durch Milane verschont. Alljährlich kreisen die Milane über dem Dorf, ohne dass wieder einer einen Raub gewagt hätte. Alle Klagen über Milanschäden sollten deshalb stets sorgfältig nachgeprüft werden, denn wahrscheinlicher bleibt es immer, dass Habichte die Täter sind. Bei Kücken kommen aber auch oft Krähen (*Corvus* spec.) oder Elstern (*Pica pica* L.) infrage.

The Role of the Internal Rhythm of Reproduction in the Timing of Avian Breeding Seasons, including Migration

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I. Introduction

The first biologists strongly to stress the importance of internal rhythm in the regulation of avian breeding seasons were Rowan (1927), the late F. H. A. Marshall (1936, 1937), Baker and Baker (1936) and Baker and Ranson (1938). It was pointed out by some that annual breeders which reproduce regularly in the spring in one hemisphere may at first conform to their original reproduction time when transferred across the equator to another. Thus, a spring breeder in Australia would reproduce in the European autumn. Such animals generally approximately reverse their sexual season in subsequent years.

Baker and Baker (1936) made it clear, however, that internal rhythm cannot alone regulate breeding periodicity. If external stimuli did not synchronise the rhythm from time to time the cycle would get out of step with the seasons. Relatively soon the animal would inevitably come into sexual condition at an inappropriate period, *e. g.* a spring-breeding species might attempt to reproduce in autumn. Nevertheless Baker (1938, 1947) subscribed to Rowan's (1927) original suggestion that the return transequatorial breeding journey from South Africa (*e. g.* in species such as the European Swallow, *Hirundo rustica*) might be governed by internal rhythm. Neither Rowan nor Baker, however, suggested internal or external means by which such a rhythm might be regulated in order that, over the ages, the northern pre-nuptial journey would be repeatedly made at the most suitable time of the year (see below).

II. The Internal Rhythm

Without in any way discounting the importance of various external regulatory factors, I have believed that the most important single — and only universal — factor in the control of avian breeding seasons, including migration, is the internal rhythm

of reproduction. However, what a person believes, and what he can prove, are apt to be metres apart; and so most of the remainder of this contribution will be devoted to evidence of the universality of the rhythm in seasonally breeding birds, and of its apparent operation in the return of equatorial and transequatorial migrants to the breeding-site.

At the end of the breeding season wild birds become unresponsive to photostimulation (as discovered by BISSONNETTE and WADLUND, 1932) and at the same time there is cessation of spermatogenesis, production of cholesterol-positive tubule lipids, tubule collapse and an overall reduction in size of the testis. Both endocrine and seminiferous elements of the testes are now temporarily out of action. These events may occur prematurely in the Arctic, or in deserts, if the environment fails to produce the stimuli appropriate to successful reproduction. Such events, too, can be duplicated by hypophysectomy. It is perhaps worth mentioning briefly that LOFTS and MARSHALL seem now to have shown by both chromatographic and bioassay methods that this post-nuptial tubule material produces progestins, and that the so-called »regressed» testis may temporarily take on functions comparable with those of the corpus luteum.

I formerly thought it probable that the male gonad, and perhaps the anterior pituitary, becomes refractory (1951). It is now abundantly clear that the adenohypophysis (or part of the C.N.S.) does do so (BENOIT *et al*, 1953; GREELEY and MAYER, 1953) and that the testis, in fact, does not (LOFTS and MARSHALL, 1958).

The seasonal inhibition of adenohypophysial function (and the resultant lipoidal metamorphosis of the testis) is probably essentially under neural control, with external stimuli ultimately involved. We know very little indeed about what really happens. However, it is reasonably sure that the time taken for the rhythmical annual recovery of adenohypophysial function is one of the most important events in the regulation of avian breeding seasons and migration.

We do not know what factors — neural or intrinsic pituitary — allow the seasonal recovery of pituitary function. Suffice here to say that until such recovery does in fact occur reproduction is impossible. Once recovery is complete, the annual cycle can begin anew. Therefore, if a species has evolved a speedy recovery of pituitary function, it can breed again very soon provided appropriate external conditions become available (*e. g.* many desert birds and *Sterna fuscata* on Ascension Island). If, on the other hand, it has inherently a delayed recovery date (*i. e.* a prolonged *regeneration period*) the next reproduction will be delayed. The length of time taken for the recovery of reproductive function is probably susceptible to natural selection. Thus, *Sterna fuscata*, breeds four times every three years. For the above-mentioned, and other, reasons the Antarctic King Penguin *Aptenodytes patagonica* of South Georgia is able to breed only twice in every three years (STONEHOUSE, 1956). The huge Royal Albatross *(Diomedea epomophora)* breeds only every second year (SORENSON, 1950).

III. THE PRE-NUPTIAL MOVEMENT

Most spring-breeding, temperate zone species so far studied regain their reproductive function in the autumn. Winter conditions inhibit reproduction. The cycle is fully reactivated only upon the advent of the increasing daylengths of late winter and spring, as has been shown by the work of ROWAN, BISSONNETTE, WOLFSON, FARNER, BURGER and others.

It has become a commonplace to say: »But what about equatorial birds and transequatorial migrants that winter above, or *below* the equator where light would be decreasing.«

First, transequatorial birds. The Short-tailed Shearwater *(Puffinus tenuirostris)* flies each autumn from its warm Tasmanian breeding islands to Japan, and thence to the South Arctic and Aleutians. Here it pauses for some months feeding on plankton, sometimes being seen perching on icebergs. Then, in August, the vast flocks suddenly start off down the west coast of North America, cross the Pacific to Australia and reach Tasmania in September during the spring. On arrival, the males are already in almost full spermatogenesis, and the females have enlarged oocytes. MARSHALL and SERVENTY (1956) wondered whether it is decreasing daylengths that start the petrels on their return journey from the northern hemisphere. It will be recalled that HOOVER and HUBBARD (1937), and subsequently others, altered the sexual cycle of brook trout, and BISSONNETTE (1941) that of the domestic goat and YEATES (1949) changed the breeding season of southdown sheep with decreasing daylengths.

However, under experimental conditions there emerged unequivocal evidence of the operation of an internal rhythm. One cage of birds was kept under artificial daylengths equalling those to which the wild birds are exposed while making the circum-Pacific journey. The sequence was telescoped by half. The control group was left under normal Australian daylengths. In neither cage did any birds show any gonad modification. Yet the survivors of *both* cages came into sexual condition at the time when the wild birds arrived from the southern Arctic (unpublished).

Second, birds that »winter« astride the equator. The species selected were *Budytes* spp. which breed in Europe and of which many individuals »winter« on the shores of Lake Victoria in equatorial East Africa. These birds arrive in Uganda late in September. By December, while their gonads are still inactive, they start to come aphasically into bright »sexual« plumage. This colour change is apparently part of an endogenous rhythm like that of the weaver-finch *Quelea quelea* (WITSCHI, 1935, 1937). It is not apparently controlled by sex hormones. In the perpetually lush equatorial lake-side environment there are no obvious external regulators; yet (with considerable temporal variation) the »wintering« population start to come into sexual condition in March, when the days are still less than 15 seconds longer than at the December solstice. WILLIAMS and I believe that the time of migration is controlled by the date at which birds come rhythmically, yet aphasically, into reproductive condition. After a brief hormone-induced period of sexual and social synchronization

(during which their habits are seen to change) the flocks of wagtails, now individually heavily fat-laden, depart when the days are still only about 20 seconds longer than at the December solstice.

Various people have suggested that birds migrate before their gonads show seasonal changes. These observations I believe to be faulty. Sex hormones can be liberated, and yet the corresponding changes in the testis may not be seen unless very carefully looked for. In this context an observation of WITSCHI (1945) is of importance. He has pointed out that the change of bill colour from black to yellow in the Common Starling *(Sturnus vulgaris)* is a most delicate indicator for androgens: it »heralds the start of the breeding season at a time when testicular changes are barely observable under the microscope, and the deferent ducts still remain in the eclipse condition». The recovery of beak colour in Starlings occurs about two weeks earlier in the males than in the females.

In Yellow Wagtails we have species that have evolved a prolonged period of post-nuptial sexual negativity. Quick post-nuptial recovery of reproductive function would bring them from their unvarying equatorial environment into the Helsinki (for example) winter. On the other hand, the Sooty Tern of Ascension Island can breed advantageously every seven or eight months. The internal rhythms of both tern and passerines can be synchronised by social behaviour (F. H. A. MARSHALL, 1936). The cycle of the Yellow Wagtails can be »anchored» annually by factors on the actual breeding ground that traditionally allow successful reproduction (MARSHALL, 1951).

It has been claimed that internal rhythm could not operate in young birds because they hatch at various times and would therefore tend to return from their wintering quarters at different, including inappropriate, times during the following year. This criticism is invalid: as already pointed out (1951), the aphasic cycles of young birds too, can be synchronised by display.

That young individuals of at least some species come rhythmically into breeding condition has been proved by VAUGIEN (1952, 1953) and by MARSHALL with DISNEY (1957) and SERVENTY (1958). VAUGIEN took young males of the Australian Budgerygah *(Melopsittacus undulatus)* shortly after they left the nest and divided them into three batches which were respectively placed 1. under natural European daylengths, 2., in continuous light and 3. in complete darkness. Samples of each group were killed for examination after 52 and 84 days. Spermatozoa had appeared within 52 days in all birds killed in each group (a total of 14 individuals). After 84 days the four survivors under continuous light contained only primary spermatocytes. Of the five birds under natural daylengths four held spermatozoa and the remaining individual only primary spermatocytes. Yet the six survivors in total darkness all contained spermatozoa.

From these results VAUGIEN concluded that total darkness seems to favour spermatogenesis in *Melopsittacus*, and that continuous light, on the contrary, appears to retard it. He was of the opinion that such results might find »une interpretation dans les origines exotiques de cet oiseau».

The Budgerygah is a xerophilous form that in many areas breeds only after rainfall and irrespective of the season (MARSHALL, 1955). Therefore, although one could readily imagine that it might fail to respond to light, there is no factor in its environment to suggest that its sexual development could be enhanced by darkness.

SERVENTY and I (1956) seem to have shown that VAUGIEN's more puzzling result is due to a misinterpretation — that his continuously illuminated birds, far from being retarded, had been photostimulated right through one spermatogenetic cycle into the beginning of another with the production of spermatocytes. But there can be no mistake about VAUGIEN's very important other conclusion — that the young parrots will quickly achieve full spermatogenesis in complete darkness.

We have found this to be true also of the males in a second xerophilous species, the Zebra Finch *(Poëphila castanotis)*. This ability of young birds quickly to reproduce is a physiological aspect of drought adaptation. These dry-country species may be unable to breed for a period of several years during a prolonged drought. When rain finally falls, and the country becomes green and full of grass-seeds, reproduction is rapid and repetitive; and even the newly hatched young come quickly into reproductive condition, irrespective of the movement of the sun.

One does not, of course, suggest that young *Zonotrichia* or *Fringilla coelebs* would behave like Budgerygahs and Zebra Finches. Neither does one suggest that adult *Zonotrichia*, kept in winter daylengths in North America, would come rhythmically into *zugunruhe* although they may in fact do so! There has been no need for it to evolve any such endogenous response since extensive daylength fluctuations occur, and can be utilized, throughout its range. LOFTS and I recently kept migratory European Bramblings *(Fringilla montifringilla)* under winter daylengths ($8\,^1/_2$ hours). On May 15, about three weeks after the wild birds had left for Scandinavia and Siberia, fat content was about 22 per cent of the total body weight but there was no *zugunruhe* and no gonad enlargement. We then increased daylength to $14\,^1/_2$ hours, equalling that of mid-April, and the gonads enlarged slightly and the birds became restless within a mere three days. It would be interesting to let *Zonotrichia* and *F. montifringilla* remain indefinitely under winter daylengths and to measure *zugunruhe*, if any, meanwhile killing off samples. After all, the Pekin ducks of BENOIT *et al.* (1956 a, b,) preserved an internal rhythm in darkness even though the amplitude of the cycle was changed.

IV. THE POST-NUPTIAL MOVEMENT

So much for movement *to* the breeding ground. What about the journey away from it — the contra-nuptial movement? BULLOUGH (1942, 1943) holds that in northern breeders the urge to migrate south is induced or allowed by a deficiency of sex hormone. He has claimed that, in resident British races of species that are migratory on the European continent, the urge to migrate has been »overcome by the autumn activity of the anterior pituitary gland which causes gonad growth and sex

hormone secretion». At the same time, however, BULLOUGH writes of an »unexplained recrudescence of sexual behaviour» in continental starlings in September, just before migration.

I have always believed that something rather more positive than the absence of sex hormones is responsible for the contra-nuptial migration. It is, I submit, the result of an inherent neural drive that operates at a certain time after reproduction despite the almost certain *presence* (in the Starling at least) of sex hormones and, in certain other species, in the presence of at least a post-nuptially reconstructed interstitium (LOFTS and MARSHALL, 1957).

Like that of *Zonotrichia* (WOLFSON, 1945, MILLER, 1948, FARNER and MEWALDT, 1955), the internal rhythm of the European Starling, Rook *(Corvus frugilegus)* and numerous other species, becomes spontaneously reactivated at the end of a more or less fixed period of negativity that follows reproduction. In resident British birds, inherently »stationary» in a relatively mild climate, autumn display finds prolonged expression. In continental migrant races, this rhythmical autumnal display (manifest in at least some species) is probably over-ridden by pre-migratory flocking activity and by the innate and overwhelmingly urgent drive to migrate.

V. THE »TIMING» OF THE BREEDING SEASON

Granted that internal rhythm is of universal occurrence in wild birds, and that at least some species start their journey to the breeding ground in obedience to it, how, and where, and how *often* is the cycle »anchored» to the environment and therefore in time?

In most species the rhythm is ultimately »timed», at the period of its seasonal culmination, by the external factors that allow nidification, incubation and successful reproduction *on the habitual breeding ground* (MARSHALL, 1951). The cycle of the Yellow Wagtail that migrates from equatorial Lake Victoria is probably »anchored» by factors that allow it to nest in Scandinavia. Probably hundreds of both stationary and dispersive xerophilous species — far more than is usually realized — are so dependent on these nest-site conditions that they reproduce only intermittently and when such conditions appear — and, in fact, almost every time they appear (*e. g. Quelea*, Budgerygah, and Zebra Finch). THOMPSON (cited by FARNER, 1955) too, has written of the possibility that the annual cycle is »linked at only one point with environmental stimuli».

On the other hand, many temperate zone species, though their cycle too, is ultimately »timed» on the breeding ground, have a subsidiary »anchor», as well as stimuli, in daylength changes, often while they are thousands of miles away from the breeding ground.

SUMMARY

The most important single — and only universal — factor in the regulation of avian breeding seasons, including migration, is the internal rhythm of reproduction that is annually and spontaneously renewed after a *period of regeneration* that follows

each breeding season. The time of reactivation is very nearly regular within each species but it varies greatly between species. In most temperate zone species so far studied the rhythm starts in very late summer or autumn, but the state of the environment then usually allows no more than autumnal sexual behaviour. External *inhibitors* depress such behaviour. This abortive autumnal sexuality represents the *primary sexual season* and is under rhythmical control. The subsequent productive sexual season of late winter and spring is generally a *secondary reactivation* that is regulated by external stimuli, including particularly photofluctuations. The time after reproduction at which the internal rhythm of reproduction is primarily renewed has been dictated by natural selection. Thus, *Sterna fuscata* in tropical Ascension Island can breed four times every three years in an equable environment apparently producing a constant food supply. On the other hand, the European Yellow Wagtails *(Budytes spp.)* that start their return from the equator in April (when the days are only 20 seconds longer than at the December solstice) have evolved a longer period of sexual negativity. The primary reactivation of their rhythm carries them north only after the termination of the European winter. Again, experimental evidence is presented showing that Shearwaters *(Puffinus tenuirostris)* which leave the Aleutian islands in the northern autumn to arrive in Tasmania to breed in the Southern spring are not influenced by decreasing light but, in fact, come into sexual condition as part of an endogenous reproductive rhythm. In each species investigated the rhythms of individuals are slightly out of phase and are presumably synchronized by sexual display. The actual time of reproduction (and therefore the »anchoring» of the rhythm to the seasons) is in most species governed by local factors conducive to nidification and the successful production of young. The cycles of temperate zone species possess a second external regulator in the increasing daylength of spring.

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An Examination of Basic Data from Wildfowl Counts

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INTRODUCTION

Wildfowl Counts are carried out on a considerable scale in Denmark, Germany, Great Britain and the Netherlands, and to a lesser extent in a number of other countries. In Britain alone the duck on more than five hundred areas of water are counted once a month over the winter. A mass of numerical data is accumulating, but so far there has been no attempt to investigate the assumptions on which the counts are based. The present paper, though based on limited data, is offered in the hope of stimulating further work on this subject.

One of the main aims of the Wildfowl Counts is to provide an objective picture of the fluctuations in wildfowl populations and, particularly, of any long-term trends. Total numbers can only be determined if the proportion of waters which are being examined is known. This, and a thorough assessment of the representativeness of the sample of waters, must wait on a detailed survey of wildfowl habitat. For the moment we are concerned with testing the assumptions that errors due to the spacing of the counts, to the mobile nature of the birds and to the estimation of numbers, will in each case cancel out. Certain assumptions as to the optimal timing of wildfowl counts can also be tested.

MATERIAL

Data were accumulated by the untiring efforts over three seasons of Miss E. M. Palmer at Durleigh Reservoir in Somerset. This was frequented by a reasonable variety of species in numbers large enough to be amenable to standard statistical analysis but not so large as to bring in unusual counting difficulties.

The reservoir covers some 35 hectares and all parts can be easily viewed. Three sides are natural, the fourth being the closing stone and concrete dam. There is good feeding for surface and diving ducks, *i. e.* it does not just serve as a roosting site. The reservoir lies within 10 kilometres of the coast so tide effects on the movements of ducks can be studied.

In three seasons, *i. e.* late July to early April, Miss Palmer counted the duck present on 565 days, and in the last two seasons hardly a day was missed. For comparative purposes additional, much less complete, material from Barn Elms and Lonsdale Reservoirs in London (108 counts), and Blagdon Reservoir in Somerset (67 counts), is also used. These data were collected by teams led by Mr. D. A. Pomeroy and Mr. B. King respectively.

The distribution of these counts in »months» centred about the international Count Dates is shown in Table A. 1 (p. 490). Hitherto the Count Date has been the Sunday nearest the New Moon. The mean counts for each month are set out in Tables A. 2 and A. 3. In the present analyses, groupings which contain less than five observations or for which the average count falls below 20, have been discarded.

THE RELIABILITY OF THE MONTHLY COUNT

When a near daily count has been made, the mean value of these counts gives a good measure of the population level within the month. If this is compared with the single count made on the actual Count Date there is often a wide deviation. In Table 1 this is shown as a percentage deviation from the »true» mean. The monthly count errs, on the average, by between a quarter and a half of the monthly mean value. But if the sign of this deviation is taken into account (algebraic mean) there is a marked degree of cancelling out, *i. e.* over a long series the monthly counts give a reasonably accurate picture of population levels, even though individual counts are unrepresentative.

TABLE 1

Reliability of Monthly counts: Durleigh, three seasons

Species	Months	Daily Counts	Mean Deviation of monthly count from average for month		Mean Coefficient of Variation (V) within months
			Arithmetic	Algebraic	
Wigeon	11	229	41 %	—6 %	88
Pochard	11	247	51 %	—7 %	76
Mallard	15	334	45 %	—14 %	75
Shoveler	5	88	41 %	—21 %	62
Teal	17	340	38 %	+15 %	56
Tufted Duck.....	19	385	25 %	—8 %	35
Mute Swan	5	122	13 %	+13 %	24

The arithmetic mean deviation is higher for some species than others, reflecting a greater instability in their populations at Durleigh. A better measure of this instability is the coefficient of variation (V), the ratio of the standard deviation to the mean, expressed as a percentage. The species in Table 1 are arranged in decreasing order of V, in the right-hand column. The value of V is not wholly a species characteristic, but will be affected by the topography of the water, its degree of dis-

turbance, relation to migration flyways, etc. Therefore similar extensive data from other waters are badly needed. The limited data from Blagdon give similar values for Teal (59) and Pochard (75), but a higher value for Tufted Duck (50) and a lower one for Mallard (37). The data from Barn Elms and Lonsdale agree with the last two values (Tufted 49 and 62; Mallard 34 and 45). It would not be fruitful to dwell on these differences as there are insufficient data available to test the many hypotheses that readily come to mind. Certainly great care should be used in drawing any far-reaching conclusions from what may be an atypical situation.

THE EFFECT OF CHANGING THE FREQUENCY OF COUNTS

The Mute Swans on Durleigh provide a useful base line as during July the majority are flightless and the population of these easily countable birds is very stable. Values for V are then around 15. In normal statistical procedure one would tend to reject data for which V was much above 30. Under Durleigh conditions only the Swan and Tufted Duck populations on that water are sufficiently stable to be adequately described by monthly counts. The stability of the population is affected by short-term fluctuations, such as caused by disturbance, feeding flights and movement in and out of cover; by medium term fluctuations caused by weather movements; and by long term fluctuations caused by seasonal migrations. The effect of changing the frequency of counts can be estimated by dividing the data into periods of varying lengths and calculating values of V for such periods. These values, as percentage deviations from the monthly value, are given in Table 2.

TABLE 2

Coefficients of variation, related to monthly values, for periods of varying length: Durleigh, 1956/57 and 1957/58

Period		Mallard	Teal	Wigeon	Pochard	Tufted	Change in V needed for effort/result to be equated
Weeks	No.	48	36	25	28	40	
	Average V	— 6 %	—35 %	—44 %	—48 %	+ 3 %	— 75 %
Fortnights	No.	26	35	14	16	22	
	Average V	— 3 %	—18 %	—32 %	—23 %	—15 %	— 50 %
Bimonths	No.	6	7	5	4	6	
	Average V	+12 %	+37 %	—13 %	+ 5 %	+28 %	+100 %
Seasons	No.	2	2	2	2	2	
	Average V	+80 %	+73 %	+19 %	+10 %	+35 %	+700 %

Neither Mallard nor Tufted Duck show an increase in stability within the shorter periods, indicating that short term fluctuations are the major cause of instability, though, of course, the level of such fluctuations is very different in the two cases. Wigeon show a definite improvement when counting is increased to once a fortnight,

and Teal and Pochard when it is increased to once a week. In these cases medium term fluctuations are being eliminated by increased frequency of counts.

In general, counts at Durleigh would have to be made at weekly intervals to show much increase in accuracy, and then not in two important species. The effort required to make the counts must also be taken into consideration. If the number of counts is doubled we would require the level of V to be halved for the effort/result ratio to be equated. Table 2 shows this equation is not reached in any species.

Within bi-monthly periods the level of V differs little from that for monthly periods in Mallard, Wigeon and Pochard, and not excessively so in Tufted Duck and Teal. Within the season as a whole the value of V rises very markedly only for Mallard and Teal, and even there the monthly value is not doubled.

THE EFFECT OF MULTIPLE COUNT POINTS

The previous section has emphasised the importance of short-term fluctuations in the general level of instability. The assumption that movements of birds between waters would cancel out can be tested by comparing the mean monthly V for two separate waters counted on the same days with that for the two waters considered as one unit. For Lonsdale and Barn Elms Reservoirs, only a kilometre apart, a big reduction in V is obtained, as shown in Table 3. Reductions of the same order, from a quarter to a half the average value for the two separate waters, are obtained by combining the results for Durleigh and Blagdon Reservoirs, 30 km. apart. This does not necessarily mean that there is an interchange between these two waters, but at least it indicates that fluctuations in different senses are occurring on them, and are cancelling out to some extent.

TABLE 3

Reduction in the mean of monthly values of V by combining data from two waters

	Mallard	Teal	Pochard	Tufted Duck
Lonsdale & Barn Elms				
Months (days)	7(48)		2(15)	6(41)
Separate V	40	—	78	54
Combined V	27	—	37	39
Durleigh & Blagdon				
Months (days)	6(51)	5(42)	3(19)	4(24)
Separate V	63	64	71	41
Combined V	33	48	43	31

THE SELECTION OF COUNT DATES AND TIMES

There would be advantages in arranging for the wildfowl counts to take place when the population was most stable. A number of phenomena, particularly weather, affect stability, but as they are unpredictable they need not be analysed in this

context. Predictable phenomena — time of year, time of day, moon phase, tide state — could however be allowed for in planning if it were shown that they produced important effects.

Time of year. Changes in the value of V are set out in Table 3. While November is the most stable month for four of the species, Pochard and Shoveler do not reach their minimal fluctuations then. Certainly the regular series of monthly counts must extend over a sufficient period to accommodate all species being investigated.

TABLE 4

Changes in the monthly value of V through the season Durleigh: mean values for three seasons

	Mallard	Teal	Wigeon	Shoveler	Pochard	Tufted
July	60	—	—	—	—	—
August	89	—	—	—	—	—
September	97	59	—	—	—	—
October	61	50	—	—	77	58
November	32	30	53	—	87	27
December	77	49	98	—	85	30
January	65	49	99	81	48	26
February	69	63	79	60	65	39
March	60	116	103	56	101	35

Time of day. The monthly data were split according to whether the counts took place in the forenoon or afternoon, finer dissection not being possible if the groupings were to contain a sufficient number of observations, fairly equally divided (Table 5). Only Mallard and Wigeon showed any noticeable effects, both giving rather few birds and more variation in the afternoon. No strong preference for morning counts is indicated.

TABLE 5

Average monthly counts and variations split according to time of day, moon phase and tide state Durleigh 1956/57 and 1957/58

	Mallard		Teal		Wigeon		Pochard		Tufted	
	No.	V	No.	V	No.	V	No.	V	No.	V
Forenoon	74	69	147	57	89	83	76	52	40	29
Afternoon	52	86	148	59	68	102	82	65	39	35
New Moon	59	81	171	41	64	57	59	47	42	31
Full Moon	74	73	170	52	103	67	60	47	42	28
High Tide	74	66	149	59	89	79	75	66	39	30
Low Tide	61	85	150	57	107	82	83	59	40	35

Moon Phase. Splitting the monthly data according to whether the count fell at the time of New Moon ($\pm$ 7 days) or Full Moon ($\pm$ 7 days) only demonstrated a difference in numbers present (more at Full Moon) in Mallard and Wigeon (Table 5). Variation was slightly greater at Full Moon in Teal and Wigeon. This is not in accord with ideas that variation should be much greater at Full Moon on account of increased migration activity and nocturnal feeding.

Tide state. The monthly data could be split according to whether the counts were near High Tide (± 3 hours) or Low Tide (± 3 hours) (Table 5). Again only Wigeon and Mallard showed any effect. The former produced more birds at low tide, the latter less, and rather more variability. The indications are that tide conditions had little effect on duck frequenting an inland water only 10 km. from the sea.

THE ACCURACY OF VISUAL ESTIMATES OF NUMBERS

The Durleigh observations concerned moderate numbers of birds in a reasonable situation for observation. *Counting* of the individual birds would thus be possible, as it is for perhaps the majority of counts in Britain, and errors from this source would be small. When large numbers of birds are present, when they are restless or liable to disturbance, or when they are actually in flight it is necessary to have recourse to *estimates*. The accuracy of such estimates has been the subject of much discussion but little attempt has been made to obtain concrete information.

Accordingly a set of twelve first class black-and-white photographs of geese *(Anser brachyrchynchus)*, both in flight and on the ground, were prepared in full plate size. These were given to the persons under test in a fixed, random order. Only one picture was shown at a time, and a maximum of 30 seconds was allowed for each estimate. The subjects were not told the correct answers until they had completed the whole series. The numbers of the birds on the photographs varied from 71 to 948, a range likely to be encountered in Britain. 117 persons, all of a reasonable educational standard, were tested, divided into three sub-equal groups:

A	Counters	(47)	having considerable experience of counting and estimating birds.
B	Watchers	(34)	having no especial experience, but enthusiastic students of birds.
C	Lay persons	(36)	with no particular interest in birds.

TABLE 6

Distribution of errors and standard deviations in visual estimates of the numbers of geese on 12 photographs

Average percentage error

Group	10—20	—30	—40	—50	—60	—70	—80	—90	—100	Over 100
A	6	21	17	3	—	—	—	—	—	—
B	2	15	12	4	1	—	—	—	—	—
C	1	5	15	8	—	1	2	1	—	3

Standard deviation of percentage errors

Group	10—20	—30	—40	—50	—60	—70	—80	—90	—100	Over 100
A	16	16	10	5	—	—	—	—	—	—
B	2	15	10	1	5	—	—	1	—	—
C	8	10	6	2	1	—	3	1	—	5

The average errors are shown in Table 6. The Counters had a mean error of 29 %, only slightly better than the Watchers with 32 %. Even the Lay group, if we omit the three quite hopeless characters who apparently had no conception of numbers, returned an average of 40 %. The Counters do show somewhat more consistency in their errors. They returned an overall mean standard deviation of 27 % as against 35 % for Watchers and 63 % (omitting the 5 in excess of 100 %) for the Lay group. The suggestion is that the small reduction in actual errors with field experience is due to a lack hitherto of any concrete standards (such as photographs) against which the estimates could be judged.

From a relatively low level, there was no tendency for the errors to become proportionately larger as the numbers of birds to be estimated increased (Table 7), There is a tendency for the individual estimates of the numbers on any one photograph to cancel each other out. There are exceptions, which may well be due to the configuration of the flock concerned. The photographs consistently underestimated (176, 736, 948) all had birds bunched together, in the one over-estimated (204), they were spread in a long skein. Much more work is clearly needed on these and other aspects of number estimation. But for the present purposes the overall tendency for errors of estimation to cancel out is the most important result. For the whole set of 12 photographs the mean algebraic errors were A −9 %, B −12 %, C −3 %. With a large number of observers, then, even data based on estimates, and not on actual counts, should give a reasonably accurate picture of a sample population. This will not be the case where a few observers are responsible for counting disproportionately large sections of the population, *i. e.* where there are immense local concentrations of birds, or where the observers are engaged in aerial survey. In such cases every effort should be made to improve the accuracy and consistency of their estimates. The use of photographs both for training and as standards in the field appears promising. The limitations of still photographs are fully recognised, but there are great difficulties in obtaining good cine-films where a flock of known size is held within the confines of the lens for a reasonable time.

TABLE 7

Relation of estimation errors to increasing size of flock

Actual numbers of geese on photograph

	Group	71	100	141	157	176	204	265	298	458	589	736	948
Mean arithmetic percentage error	A	10	21	24	24	36	34	35	28	34	31	33	37
	B	10	18	25	26	39	40	35	30	33	43	40	42
Mean algebraic percentage error	A	—5	—11	—10	— 8	—33	+20	+6	—6	—5	—9	—21	—21
	B	—1	—12	—11	—14	—35	+24	—9	+5	+2	—9	—37	—29

CONCLUSIONS

The original assumption that errors from various sources in the wildfowl counts will tend to cancel out appears to have been justified.

As the present data are limited in scope it would be unwise to use them to advocate changes in the frequency and timing of the counts.

Similar investigations from other areas are needed.

Summary

1. Nearly daily counts were made over three seasons on one reservoir, and supplemented by less full data from three others.

2. Measures of the reliability of monthly wildfowl counts showed differences between species.

3. Changing the frequency of counts had some effects on their reliability.

4. Fluctuations of birds tended to cancel out between waters.

5. Populations become more stable at certain times of year.

6. Time of day, moon phase and tide state did not appear to affect the stability of the duck population.

7. The accuracy of visual estimates of numbers was tested by using photographs. Persons with much field experience were more consistent but the level of error was high. Errors made by different individuals tended to cancel out.

ACKNOWLEDGEMENTS

The British wildfowl counts in general, and this analysis in particular, are made possible by grants from the Nature Conservancy. The Water Boards concerned were most helpful in permitting access to their reservoirs.

The fundamental debt owed to the work of Miss E. M. Palmer will have been apparent, while valuable supplementary data were provided by Messrs. D. A. Pomeroy, B. King and their helpers.

APPENDIX

TABLE A. 1

Distribution of counts within periods of ± 15 days of the count dates

	Durleigh Reservoir			Lonsdale	Barn Elms	Blagdon
Month	1955/56	1956/57	1957/58	1949/50	1941/50	1956/57
July	—	23	30	—	—	9
August	7	31	31	—	—	15
September	5	30	31	6	6	10
October	9	30	30	7	7	9
November	14	22	26	7	7	7
December	14	20	25	8	8	4
January	11	28	22	7	7	6
February	14	30	26	7	7	5
March	8	22	27	6	6	2
April	9	—	—	6	6	—
	91	236	238	54	54	67

TABLE A. 2

Average number of birds counted in the periods ± 15 days of the count dates at Durleigh Reservoir

	Season	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Febr.	March	April
Mallard	55/56	—	88	150	13	14	11	6	56	30	8
Anas platyrhynchos	56/57	15	78	136	82	87	22	22	8	5	—
	57/58	48	131	86	19	19	12	31	22	18	—
Teal	55/56	—	5	14	67	82	89	126	167	132	10
Anas crecca	56/57	0	17	41	102	170	263	95	17	12	—
	57/58	<1	3	14	39	174	334	297	93	38	—
Wigeon	55/56	—	0	<1	<1	1	1	201	417	173	18
Anas penelope	56/57	0	0	0	12	37	36	45	18	2	—
	57/58	0	0	0	0	40	75	156	110	139	—
Pintail	55/56	—	0	0	<1	0	0	2	16	7	<1
Anas acuta	56/57	0	0	0	0	0	6	9	2	12	—
	57/58	0	0	0	0	2	1	7	4	19	—
Shoveler	55/56	—	0	0	<1	8	7	62	46	59	11
Anas clypeata	56/57	0	0	0	0	10	15	19	1	0	—
	57/58	<1	<1	<1	<1	<1	2	5	20	39	—
Tufted Duck	55/56	—	0	0	24	44	53	28	36	42	27
Aythya fuligula	56/57	0	<1	7	27	50	40	65	72	31	—
	57/58	2	5	8	28	42	32	28	31	25	—
Pochard	55/56	—	2	<1	7	36	36	68	113	84	11
Aythya ferina	56/57	0	3	6	75	65	81	142	86	2	—
	57/58	<1	<1	2	11	28	18	19	19	11	—
Mute Swan	55/56	—	89	27	3	<1	0	1	4	2	2
Cygnus olor	56/57	49	28	10	10	9	6	6	2	7	—
	57/58	54	35	18	13	4	3	8	2	2	—

N.B. Smaller numbers of Goldeneye *(Bucephala clangula)*, Smew *(Mergus albellus)* and Goosander *(Mergus merganser)* also occurred.

TABLE A. 3

Average number of birds counted in the periods ± 15 days of the count dates at Lonsdale and Barn Elms in 1949/50 and at Blagdon in 1956/57

	Reservoir	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Febr.	March	April
	Lonsdale	—	—	93	55	32	67	104	51	30	14
Mallard	Barn Elms	—	—	66	65	56	92	174	178	99	55
	Blagdon	214	207	202	262	243	231	172	140	64	—
Teal	Blagdon	4	49	209	541	692	499	296	41	64	—
Wigeon	Blagdon	—	—	1	142	207	104	87	145	119	—
	Lonsdale	—	—	10	21	97	139	172	248	98	25
Tufted	Barn Elms	—	—	57	16	26	289	548	284	31	27
	Blagdon	0	35	132	204	207	139	91	106	83	—
	Lonsdale	—	—	5	<1	16	38	21	7	0	0
Pochard	Barn Elms	—	—	24	54	141	161	280	94	2	<1
	Blagdon	—	4	32	457	192	140	19	53	38	—

On the »Atlas of Distribution of Palaearctic Birds»

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Berlin

Ornithologists familiar with faunistics are aware of the large gaps in our knowledge of the distribution even of European birds. Wide areas of, for instance, Greece, Romania, or Norway are practically unknown.

If information is wanted on the breeding distribution of any species, the handbooks will usually be consulted. The precise outlines of the range, however, are not always recognizable from these, for they are based upon political frontiers. Information considerably more reliable is to be gained from distribution maps, of course, but one wonders why this useful method has been so little used. It is true that some attempts to plot the areas of single bird species (more or less exactly) have been made. The first ornithological handbook to map consistently all species dealt with in it is the six-volume work on »The Birds of the Soviet Union» by Dementiev and Gladkov. The tiny maps in the »Field Guide to the Birds of Britain and Europe» cannot offer more than a rough survey. But all these maps, even if correct, suffer from the lack of fully documented boundary points which prove the reliability of the limit. Of course, exact mapping takes very much time and this method could hardly be used for a large handbook like the Russian one.

There is a pressing need to survey the recent improvements in avifaunistics and, at the same time, to supply basic and new information indispensable for further investigations. Both these aims are to be attained by the »Atlas of Distribution of Palaearctic Birds» that will be edited, under the auspices of the German Academy of Sciences, by Prof. Dr. Stresemann and with the preparation of which I have been charged.

This is not a task to be undertaken by one person only; its size demands very close international co-operation. We therefore have the permanent aid of Prof. Portenko, who is an outstanding expert in avifaunistics and ornithogeography of the Soviet Union that constitutes a huge part of the Palaearctic Region. He will be named as co-editor of the Atlas. For about one year Dr. Eber and Dr. Szijj of Bonn were also occupied with the preparation of some maps.

In a work of this character it is necessary not only to trace the literature as completely as possible, but also to appeal to as many correspondents as possible for detailed information. My numerous applications to specialists in many countries

have always met with a ready response and we gratefully acknowledge the assistance received. A good number of requests are necessary since many authors do not inform the reader about the position of localities mentioned in their papers and they are not always to be found on any map. Authors should add either a detailed map or the geographical co-ordinates of localities the knowledge of which cannot be expected.

The Atlas will deal with about 200 bird species breeding in the Palaearctic Region. The range of each species will be shown by a two-coloured map. A text of about two pages will briefly cite the literature consulted, the range of ecological conditions under which the species occurs, the time and route of migrations and, in most cases, the degree of relationship to allied species. The work will be published in numbers containing 20 species each.

(The type of maps is briefly explained by a sample, the Citril Finch.)

The tops of the red triangles mark the limits beyond which the bird has not been recorded breeding. They are connected by a line which will thus approach closely the actual border of the range. The red numbers refer to a list giving the name of each particular locality, the kind of proof (*e. g.* whether a nest has been found or adult birds have been observed during breeding season), the approximate frequency, and the authority.

Thus the maps will show that the species in question breeds within the red border line at localities offering suitable ecological conditions (as for instance of altitude, quality of soil, or vegetation). Against this kind of map the objection could be made that it gives a wrong impression, suggesting that the bird is equally spread over the whole range circumscribed. But it should be borne in mind that the types of environment characteristic of each species are defined under the heading of ecology and offer a key to the details of distribution; thus a bird inhabiting stony arid slopes with scattered bramble vegetation may not be expected to breed in swampy lowlands. Nevertheless, it might appear more appropriate to map breeding localities separately. But such a map would suggest a degree of exactitude which in fact it was very far from possessing. It could only show those points where a published record happened to be available. Considering the immense areas of the Palaearctic Region this would provide a picture further from reality than ever. Despite this, however, we are constrained to use this method for those species whith are either rare or scattered, or which live mainly in countries which are almost unexplored. Finally the Atlas, although as accurate as possible is not intended to reproduce all local details, but can offer a broad survey only. For this reason the work will, it is hoped, encourage new and more detailed investigations, not only into faunistics, but into taxonomic questions arising out of particular distribution, and for special studies of ecological conditions. With regard to particular studies in breeding biology and ethology new questions are raised, the solutions of which are closely connected with taxonomic considerations. So, for example, the uncertainty of the systematic position of the Semi-collared Flycatcher *Muscicapa semitorquata* is being removed by a

detailed ethological study suggested by the distributional relations of the three European black-and-white flycatchers. Furthermore, in some species the position of the breeding range and of the winter-quarters raises new problems in migration research. And lastly, the accurate maps will be of service to the evolutionist.

The Atlas will meet a requirement that has long been acutely felt. It is an innovation not only in ornithological but in zoological literature generally. Being a work of international collaboration, it will we feel sure prove of great interest.

Chairman's Introduction to the Symposium on Adaptive Evolution

Ernst Mayr

Harvard University

We celebrate this year, 1958, the centenary of the publication by Darwin and Wallace of the theory of evolution by natural selection (1858). It would seem appropriate under the circumstances to devote a symposium at this year's International Ornithological Congress to a discussion of one of the major problems of evolution. When asked by the General Secretary of the Congress to organize such a symposium, I felt that there is no other problem as challenging as that of adaptation. A study of the many-sided adaptations of birds to their environment would have the additional advantage of permitting a discussion of some of the most fascinating aspects of current research in avian morphology, physiology and ecology.

Adaptation is not a simple problem that can be solved by a relatively simple answer, such as mutation or isolation. Adaptation is a temporary balance between the numerous demands made on an organism by the environment; or, to express it in terms of modern evolutionism, it is a compromise between many selection pressures, some occasionally quite antagonistic to each other. In order to understand how such a compromise can be reached, we must give a short summary of the current status of the evolutionary theory.

One hundred years is a long time in the short memory of man, and the changes in the evolutionary theory during this period have been truly astonishing, notwithstanding the fact that in some ways we are today closer to Darwin's original concepts (1858—59) than were the evolutionists at any other time during the past 100 years. A symposium devoted to the identical topic of the adaptation of birds, held only 30 years ago would have limited itself, presumably, mostly to morphological characters and much time would have been wasted in a misunderstood argument whether Darwin or Lamarck had been right.

What we have learned since then has clarified the issue so completely that virtually no more room for argument is left, as far as the basic mechanisms of evolution are concerned. There has now emerged a synthetic theory of evolution, as Huxley has called it (we could also call it an eclectic theory), which has selected the best elements of previously feuding and competing theories and has combined them

into a harmonious whole. It may help our thinking and simplify our discussions to summarize the essential conclusions and theses of this eclectic theory.

(1) The genetic material is the nucleoprotein of the chromosomes in the nucleus of the cells. The specific chemical structure of this material determines the genetic properties of an individual.

(2) The individual and its organs, the »phenotype», is the product of an interaction of ten thousands of genes with each other and with the environment.

(3) Each natural population contains a great variety of such genes, in each generation reassorted (»recombined») in an infinite variety of genotypes.

(4) Some of these genotypes are »superior» in one way or another in the environmental constellation in which they occur in space and time, and have thus a greater statistical probability to survive until they reach reproductive age and to leave a greater number of offspring (»differential reproductivity»). This statistical process is called »natural selection». It merely describes, as was correctly pointed out by DARWIN himself, an observable fact.

(5) The steady loss of genetic variability by natural selection is compensated for by »mutations», that is: the occasional discontinuous change of genetic factors. The majority of mutations are, according to the best estimates of geneticists, of slight effect on the phenotype and can be recorded only by special methods.

(6) Mutations do not cause evolutionary trends or evolutionary novelties as such. They merely replenish, so to speak, the genetic reservoir.

(7) Evolutionary trends and novelties, and hence all adaptations, are under the steady control of natural selection.

I thought that such a short statement of the current evolutionary theory might help to eliminate misconceptions that might still be in existence. If I may speak for a moment, as a naturalist, I would like to emphasize the enormous downgrading in the last fifty years of mutation as an evolutionary factor. To be sure, all genetic variation is, by definition, the result of mutation. Yet, the evolutionary change as such is not the result of individual mutational events, but of the molding effect of the environment. And, since this is something we can study directly, and without need of a detailed genetic analysis, we can make significant contributions to the elucidation of the process of adaption merely by an analysis of the selective factors of the environment and of the adaptive mechanisms themselves.

The new insight into the nature of genes and genotypes facilitates an understanding of several aspects of adaptation. For instance, it helps to answer the question, »What is an adaptive character?», or perhaps better, »Are there any non-adaptive characters?» We now realize that not every aspect of the phenotype is necessarily adaptive. What is being selected is the total phenotype and through it the total genotype! A given gene may have manifold effects in the organism, indeed, we know that perhaps the majority of the genes are what we call »pleiotropic», that is, that they affect simultaneously several or many organs. As a consequence, a highly valuable gene, a gene of high selective value, may result in phenotypic by-products

which are selectively neutral. Thus, some aspects of the visible phenotype may not be of adaptive significance, even though the genotype which produced it is the result of selection.

A second point, always to be kept in mind, is the fact that the phenotype is always a compromise between several opposing selection pressures. And this is even more true for the features of the physiological than those of the morphological phenotype. Clutch size is such a compromise, as shown by LACK. Wing and bill size is another as shown by DAVID SNOW. The study of the feeding behavior of Herring Gull chicks by TINBERGEN has shown that a much larger and more contrastingly colored bill would result in an even stronger feeding response of the young chick. Such a bill, however, would be unsuitable for food gathering by the parents, and, as a consequence, natural selection has achieved a compromise. A similar conclusion is true for other superoptimal stimuli.

Let us always keep in mind that nearly all adaptations are a compromise between conflicting selection pressures.

The word adaptation, in the modern biological literature of the English speaking countries, refers to a situation, to the condition of »being adapted». I was interested, in recently going through the German evolutionary literature of the period 1900—1925, to find that all the examples which would be listed under »adaptation» in the modern literature, were recorded under »Zweckmässigkeit». The choice of this term implies at once the operation of finalistic or teleological factors, and thus prejudges the issue.

Let me therefore reiterate that, to begin with, we will use the term adaptation in a strictly descriptive sense. Anything that favors survival and successful reproduction would, by definition, be adaptive. However, as soon as we attempt a more detailed analysis, we run into difficulties. There is, for instance, the question of *special* versus *general* adaptation to which certain authors have given much thought. If we take a woodpecker, for example, we find a hierarchy of increasing specializations. There are adaptations, as found in the circulatory and the nervous system, the essential features of which the woodpecker *still* shares with the ancestral aquatic chordates; there is the respiratory system and the hard-shelled eggs, as examples of more specialized adaptations which were acquired by the first terrestrial tetrapods; there are the feathers, wings, and the other typical avian specializations which are the earmarks of the conquest of the air by birds. There are the still more special adaptations, characteristic of the family of woodpeckers, signifying the ability to climb tree trunks and to excavate nest holes, and finally and lastly there are the very special adaptations, in the feet, the tail, the bill, the tongue, and general proportions which adapt a given species of woodpecker to the particular food on which it lives and the habitat in which it occurs. Here we have a hierarchy of at least five adaptive levels, each more specialized than the previous one, and superimposed on it. You will agree with me if I state that it is a little difficult to decide where to draw the line between general and special adaptations.

Another problem concerns the relation of the adaptation of the individual to evolutionary adaptation. Every physiologist is familiar with the regulatory processes which adjust an organism after a shift from a cold to a hot climate or from a low to a high altitude. An individual can adapt himself to various environmental conditions because he is equipped with the necessary homeostatic devices and with a plastic physiology. Individual adaptability is a necessity in any changing environment and there are few environments that do not require from their inhabitants a considerable capacity for adaptation. Yet, the genetic basis remains the same through all these changes.

Adaptation within an evolutionary line is something quite different. It involves a real change, not merely a capacity to respond phenotypically. The change consists in a change of the genetic composition of a population or species and in the concomitant changes of the phenotype. These changes of genetic composition are at all times under the control of natural selection.

Nothing could be more dangerous or misleading than to try to explain evolutionary adaptation by analogy with adaptation of the individual or vice versa. The two processes have virtually nothing in common, they are based on different principles.

Birds are, for two reasons, a particularly suitable group for a study of adaptation. The first is that birds are unusually uniform in their basic anatomy, a fact to which anyone can testify who has attempted to classify birds. Yet, birds have succeeded in invading an enormous number of ecological niches, evolving there such superficially divergent types as penguins, ratites, humming birds, swifts and woodpeckers. The adaptation of the basic pattern to these highly divergent types is a fascinating chapter in the book of adaptation. Equally fascinating is the story of convergent evolution owing to repeated invasions of the same niche, as documented by the superficial similarities of diving birds, secondarily flightless birds, »fly-catchers», and various other specialists.

The second reason for the special suitability of birds for such studies is that they are so well known. What other group of animals is there in which one could demonstrate equally well that adaptation is not merely a morphological problem, as one might gather from the older literature, but that the needs for adaptation affect equally also physiology, ecology, and behavior, in short every aspect of biology?

To focus attention on this diversity of adaptation has been our special aim in organizing this symposium. In the morning session the emphasis will be on certain aspects of morphology, in the afternoon on behavior, ecology and physiology.

In concluding, I would like to express to the speakers the thanks of the Congress for the readiness with which they agreed to prepare a contribution to this Symposium.

Über Verbreitung, Verbreitungsgeschichte und Evolution afrikanischer Vögel

Wilhelm Meise

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Die Grundzüge der Tiergeographie sind kürzlich von dem Entomologen Ph. J. Darlington, jr., (1957) zusammengestellt worden. Meine erste Reaktion war Pessimismus, weil wir wohl kaum den Abschluss eines umfassenden Atlasses der Tierverbreitung erleben werden, so wenig wie die Vollendung des Lieferungswerkes »Das Tierreich» oder seines eventuellen Nachfolgers — obwohl beide Werke für den Tiergeographen und den Evolutionsforscher sehr wichtig wären.

Aus dem Pessimismus retten wir Ornithologen uns durch Beschränkung auf die Vogelwelt, die seit der Jurazeit ihre eigene Entwicklung durchlaufen hat, zum Teil darum, weil sie über andre Verbreitungsmittel verfügt als die übrigen Tierklassen. Die Geschichte der etwa 2.000 aus Afrika nachgewiesenen Vogelarten hat öfter die Forscher gereizt. Mit Hilfe der alten Brückentheorie, der Kontinentalverschiebungstheorie und der heutigen Konstanzlehre hat man sie zu enträtseln versucht, wobei man leider auf paläontologische Funde fast ganz verzichten musste. Erfolgversprechend ist die Tatsache, dass Afrika seinen äusseren Umriss seit der Kreidezeit nur im Norden wesentlich geändert hat (Moreau 1952).

Die Verbreitung afrikanischer Vögel, die ich in Angola und in Marokko selbst kennen lernte, soll hier weder im ganzen noch in ihrer vielfachen Gliederung dargestellt werden. Nach zwei Vorbemerkungen möchte ich vielmehr zwei Punkte herausgreifen, die Bedeutung für andere Gebiete zu haben scheinen.

1 a. Zunächst eine systematische und arealgeschichtliche Frage, die zwei Muscicapiden-Gattungen betrifft, *Erythrocercus* mit zwei Arten und *Chloropetella* mit einer Art. Schon vor 20 Jahren sagte mir Hermann Grote, dass dies weder Gattungen noch Arten, sondern Rassen seien. Tatsächlich sind Jugendkleider und Strukturen sehr ähnlich. Die Gefiederfärbung des Alterskleides dagegen ist sehr verschieden. Man kann wohl alle drei Arten zu *Erythrocercus* stellen und wegen der Rassenfrage weitere Forschungen im östlichen Tanganyika abwarten, wo *Erythrocercus livingstonei* Gray *E. holochlorus* Erlanger am nächsten kommt. Immerhin, die räumliche Nähe zweier so nahe verwandter und doch so verschiedener Formen weist auf eine Schranke hin, die südliche ostafrikanische Gruppen im mittleren Teil von

Tanganyika längere Zeit von nördlichen getrennt haben muss. Wegen der Anpassung der nördlichen Form an Dornbuschumwelt möchte ich eine Waldschranke, keine aride Schranke annehmen.

1 b. Der Nacktkehlfrankolin, *Pteronistes afer* (Müll.), ist kürzlich wieder in *afer* und *cranchii* geteilt worden, obwohl es in Süd-Angola deutliche Übergänge gibt (MEISE 1958, p. 64—70). Die Art gliedert sich in etwa 20 meist gut gekennzeichnete Subspezies. Vom Unterlauf des Kongostromes südwärts bis an den Kunene in Westafrika und vom südlichen Kenya südwärts an der Ostküste Afrikas sind diese 20 Rassen über den grössten Teil Südafrikas verbreitet, fehlen aber dem Norden des Erdteils. Wenn man die Kerne aller 20 Rassengebiete als Entwicklungsgebiete ansieht, könnte man annehmen, dass rings um jedes Rassengebiet zu einer gewissen Zeit Schranken gewesen sein müssten, die den Genfluss unterbrachen und die Entstehung der Rassen ermöglichten. Tatsächlich fallen viele Arealkerne, wie W. REINIG (1950) sie genannt hat, zusammen, aber ich möchte mich heute nicht auf spezielle natürliche Schranken einlassen, weil wir über die Entstehung neuer Rassen in kontinuierlichen Populationen noch gar zu wenig wissen. Hier liegt ein erstes Problem, mit dem sich die erklärende Tiergeographie auseinandersetzen muss.

Die Frage in beiden Fällen, bei *Pteronistes* und bei *Erythrocercus*, lautet: Soll man länger wirksame absolute Verbreitungsschranken zwischen gut unterschiedenen verwandten Einheiten annehmen, oder genügt die relative genetische Isolierung, in der sich Teile jeder grösseren Population befinden? Es gibt wohl keine allgemeine Antwort auf diese Frage, sobald die Populationen heute kontinuierlich verbreitet sind.

2. Nach dieser Isolationsfrage eine faunenanalytische: Wie gross ist der Anteil, den der von STRESEMANN und GROTE (1928) für den Kopenhagener Ornithologen-Kongress erarbeitete Arealtyp der S a v a n n e n r i n g e an der Gesamtheit der Vogelareale Afrikas hat? Dieser Verbreitungstyp umfasst die Hylaea im Norden, Osten und Süden, wir nennen ihn »Ring», obwohl er im Westen offen ist. Enge Ringe zogen z. B. *Smithornis capensis* (Smith) und *Estrilda paludicola* Heuglin, die also nur den wirklich dichten Urwald frei lassen, aber die Bereiche seiner Ausläufer durchdringen und in Nord-Angola vorkommen. Nicht scharf davon zu trennen sind die weiten Ringe, die am Senegal beginnen und über Eritrea bis ins Kapland ziehen, um in Südwest-Afrika wieder an die Küste des Atlantiks zu stossen: Als Beispiel nenne ich *Euplectes orix* (L.) und *Euplectes afra* (Gm.).

Nun sind 169 unter den 942 Passeres- und 208 unter den 668 Nonpasseres-Arten, meist Savannenvögel, in weiten Teilen Afrikas zu finden. Diese Passeres und Nonpasseres sind zu je etwa 70 %, zusammen 265 Arten, nach dem Typ des Savannenrings verbreitet. (Ein grosser Teil der 265 Arten, darunter 17 Passeres wie *Cyanomitra olivacea* (Smith) und *Vidua macroura* (Pallas), lebt auch in der Hylaea). Mit 16 % ist der Savannenring der Hauptverbreitungstyp afrikanischer Vogelarten. Es folgt aber, dass weniger als die Hälfte der Savannenarten ihren ganzen Lebensraum erobert haben. Bei den 46 keinen Ring bildenden weit verbreiteten Passeres-Arten fehlt meistens der Sudan-Vertreter, also das Nordweststück des Ringes — in 23 Fäl-

len —, in 9 Fällen fehlt umgekehrt der Süden und Südosten des Ringes bis etwa ins Tanganyika-Territorium nordwärts.

Auf die Probleme der Savannenringe gehe ich nicht weiter ein. Sie bestehen z. T. darin, dass hier sowohl ungeteilte als geteilte Arten vorkommen, aber auch im Norden und Süden sich vertretende Gattungen wie die Würger *Corvinella* nördlich und *Uroleuca* südlich vom Kongourwald (Meise 1958, p. 79).

3. Nun zu den beiden Hauptpunkten: Der erste, faunenanalytische, betrifft die ökologische Potenz der Gattungen. Die scharfe Trennung der Arten in Savannen-, Niederungswald-, Bergwald- und Wüstenarten geht meist nicht soweit, dass man aus dem Balg schliessen kann, wo die Art lebt. Trotzdem sind 95 % der 1,700 afrikanischen Brutvogelarten, nach den *Muscicapidae* s. l. zu urteilen, einem der vier Biome allein zuzuschreiben, also der Savanne, der Hylaea, dem Bergwald oder dem ariden Gebiet. Nach Moreau (1952, p. 890) sind 89 % aller *Passeres*-Arten Afrikas biotopmässig einseitig festgelegt. Man staunt, dass sich so wenige Arten euryök verhalten. Ich finde unter den Muscicapiden von 75 Arten 3: *Alseonax adustus* (Boie), *Parisoma plumbeum* (Hartl.) und *Batis minor* Erlanger, unter den 102 Turdiden auch 3: *Erythropygia leucophrys* (V.), *Cercomela familiaris* (Stephens) und *Saxicola torquata* (L.).

Ganz anders ist das bei den Gattungen. Von ein und derselben Gattung bewohnt häufig *eine* Art das Waldgebiet, eine zweite die umgebenden Savannen und eventuell noch eine dritte Art den Bergwald. Als Beispiele seien *Cichladusa*, eine Turdidengattung mit vier Arten, und *Pitta* mit zwei Arten erwähnt, ferner *Smithornis* mit zwei Arten im Niederungswald und einer im dichten Busch des umgebenden Savannengebietes. Unter den reich gegliederten Gattungen kommt z. B. *Alethe* im Berg- und im Niederungswald vor und fehlt den Savannen, *Bradornis* aber bewohnt Savannen und aride Gebiete.

Gehen wir von der Verbreitung der 942 Passeres-Arten aus, von denen 12 in Afrika sehr weit verbreitet sind und 38 nur in Nordwest-(Klein-)Afrika vorkommen! Etwa ein Zehntel sind reine Wüstenbewohner, ein Achtel lebt im Hochgebirge, meistens im Bergwald, ein Fünftel sind Vögel des Niederungswaldes in Nieder- und (oder) Oberguinea, und fast die Hälfte bewohnt Savannen und Steppen. Auch aus Moreau's etwas abweichenden Zahlen (1952) ergibt sich eine ähnliche Verteilung.

Man kann die 942 Passeres in 270 Gattungen unterbringen. Von diesen enthalten 124 nur eine Art — darunter 14 Paläarkten, 2 Inselgattungen, 24 Niederungswald-, 65 Savannen-, 7 Bergwald- und 12 Wüstengattungen. Die monotypischen Gattungen sind etwa wie Arten über die grossen Lebensräume verteilt, nur im Bergwald sind anteilmässig viel zu wenig, was auf dessen geringeres Alter schliessen lässt. Es bleiben 146 Gattungen. Von diesen sind 72 mit 2—3 Arten und 74 mit 4 und mehr Arten in Afrika vertreten. Die 74 reich gegliederten Gattungen beschranken sich grösstenteils nicht auf einen Landschaftstyp, sondern gehören zu mehreren Biomen. Von 13 solchen Gattungen der Hylaea kommen 10 auch in Savannen, 7 auch im Bergwald und 2 im Wüstengebiet vor, von 37 Gattungen der Savannen kommen 26 auch im

Niederungswald, 11 im Bergwald, 8 im Wüstengebiet vor — ich erwähne die Gattung *Tychaedon*, die den Regenwald mit einer, die Savannen mit 3 Arten bewohnt.

Weiter sind von 4 Gattungen der Bergwälder 3 auch im Niederungswald und eine auch in Savannen zu finden, und schliesslich von den 3 Gattungen des ariden Gebietes alle 3 auch in der Savanne. Von 74 Gattungen mit 4 und mehr Arten sind also 57, d. h. 77 %, in mehreren Biomen vertreten.

Es bleiben 17 Gattungen übrig, die zwar in Afrika artenreich sind, aber ihren Landschaftstyp nicht verlassen haben: Von Gattungen der Hylaea sind das *Dyaphorophyia, Malimbus, Nigrita,* 3 Gattungen, von Savannenvögeln 13, von Bergwaldgattungen nur *Cryptospiza* und von den Bewohnern der ariden Gebiete keine einzige Gattung mit 4 und mehr Arten. Dazu ist noch zu bemerken, dass von den 13 Savannenvögeln *Anthus, Sylvia, Monticola* und *Emberiza* vielleicht nicht äthiopischer Herkunft sind und dann nur 9 Gattungen aus den Familien der Stelzen, Würger, Stare, Webervögel und Finken übrig bleiben.[1]

Was folgt aus diesen Zahlen? Die Landvögel Afrikas haben die Tendenz (und das gilt auch für andere Erdteile), ihre Vertreter in alle möglichen erträglichen Biotope zu entsenden, sich soweit wie möglich auszubreiten. Bei den Nonpasseres-Gattungen haben allerdings nur 19 % gegen 27 % bei den Passeres 4 und mehr Arten in Afrika, aber auch von diesen reichgegliederten Gattungen sind 73 % in mehreren Biomen zu finden. Ferner fällt beim Durchblättern afrikanischer Vogelwerke (wie Bannerman 1953, Chapin 1932—54, Mackworth-Praed u. Grant 1952—55, Roberts 1940) auf, dass oft eine Steppengattung neben einer nahe verwandten Waldgattung angeführt wird, und auf diese Tatsache ist auch zurückzuführen, dass die Gliederung der Faunen nach ökologischen Vogelgruppen so unbefriedigend und fast überall wieder verlassen ist. So ist die ökologische Pluripotenz der Gattungen noch verbreiterter, als aus den Zahlen hervorgeht.

Es ergibt sich: Von den systematischen Einheiten afrikanischer Passeres sind alle Familien (ausser *Salpornis*) in mehreren Biomen vertreten. Für etwa 75 % der 109 Gattungen mit vier und mehr Arten gilt dasselbe. Von einer scharfen Aufteilung der gesamten afrikanischen Vogelwelt auf die vier Biome Niederungswald, Bergwald, Savanne und Wüste, von einer Koexistenz vier getrennter Faunen

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[1] Wir teilen die 270 Gattungen noch einmal anders auf. Von ihnen sind
56 Bewohner des Niederungswaldes, darunter 24 monotypisch, 16 mit 2—3 Arten, 3 mit 4 und mehr Arten, die restlichen 13 Arten ausser im Niederungswald noch in anderen Biomen vertreten.
146 Gattungen gehören der Savanne an, darunter 65 monotypisch, 31 mit 2—3 Arten, 13 mit 4 und mehr Arten, die restlichen 37 artenreichen Gattungen auch in anderen Biomen.
14 sind Bewohner der Bergwälder, davon 7 monotypisch, 2 mit 2—3, 1 mit 4 und mehr Arten und 4 artenreiche auch in anderen Biomen,
26 in ariden Gebieten mit den entsprechenden Zahlen 12, 11,0 und 3,
24 Paläarkten, darunter 14 monotypisch in Afrika auftretende, 4 Inselgattungen des Westens oder Ostens.

im tropischen Afrika (MOREAU 1952) kann also nur beim Betrachten der Artkategorie gesprochen werden.

4. Beginnen wir nun den faunenerklärenden, vorwiegend faunenhistorischen Teil mit ökologischen Bemerkungen über die Pluripotenz der Gattungen. Wenn auch viele Gattungen Wald und Steppe zugleich bewohnen, so sind doch die extremen Formen in beiden Biotopen verschieden: CHAPIN (1932) und MOREAU (1952) haben das gut herausgearbeitet. LÖNNBERG (1925) hat mehr von der Umwandlung der Waldvögel in Steppenvögel bei der Austrocknung Afrikas gesprochen und z. B. *Bucorvus* aus Wald-Bucerotiden abgeleitet. Wer wie ich das Glück hatte, vom dichten Regenwald am gleichen Tag auf die offenen Höhen Angolas zu kommen, der staunt, wie wenig verschieden die Vögel beider Gebiete in ihrem Habitus sind. Die ökologische Siebwirkung bedeutet hier anscheinend nicht sehr viel, absolute Schranken scheinen nicht zu bestehen. Die Vertreter von Steppengattungen sind im Waldgebiet meistens mehr in den lichteren Teilen zu finden und umgekehrt. Ich möchte auf Anpassungsfragen nicht eingehen. Trotzdem war diese ökologische Vorbemerkung notwendig zur historischen Erklärung der Pluripotenz: Im Laufe langer Zeiten sind Wald- und Steppenformen nicht scharf voneinander getrennt, also ist die Geschichte der Biotope, ihre Isolierung, für die Gattungs- und Artentwicklung nicht so einschneidend, nicht so beschränkend, wie es nach dem Studium der Rassengeschichte aussieht. Es fanden im Bereich der rezenten Gattungen so oft Habitat-Änderungen statt, dass auch paläontologische Passeresfunde nicht unbedingt auf ein bestimmtes Biom schliessen lassen. Die relative Unabhängigkeit der Gattungsgeschichte von der Biotopgeschichte ist ein Vorteil, weil wir über die Geschichte der Pflanzenassoziationen in den Tropen bisher sehr schlecht unterrichtet sind, genau so schlecht wie über die Verbreitung der tropischen Tierwelt in vergangenen Epochen. Wir müssen i. a. von der Verbreitung heutiger Formen ausgehen, was umso betrüblicher ist, als wir mit DARLINGTON (1957, p. 545—7) der Meinung sind, dass die meisten Tiergruppen in den Tropen entstanden sind. Die geringe Hilfe, die Geologie und Botanik für die afrikanische Faunengeschichte bieten können, hat MOREAU (1952) grossartig ausgenutzt, und in der Linnean Society Londons ist dieses Problem am 29. I. 1953 besprochen worden, ohne dass die Ergebnisse befriedigend wären (MOREAU 1953). Eigentlich müsste man die Hände in den Schoss legen, wenn solch ein Forschungsoptimist wie MOREAU in der *Zosterops*-Monographie (1957) Historisches ganz und gar ablehnt.

Doch bleibt es unsere Aufgabe, Vorstellungen vom Werden der afrikanischen Vogelwelt zu entwickeln und die Tradition von LÖNNBERG (1926), BOWEN, CHAPIN (1932), MOREAU (1952, s. dort Literatur), VERHEYEN (1953), RIPLEY (1957) und vielen anderen fortzusetzen.

Aus dem Endsatz unter 3. von der Pluripotenz der Gattungen folgt zunächst, dass Millionen Jahre zur Verfügung stehen müssen. Denn warum soll man annehmen, dass bei Feuchtigkeitsschwankungen gleichzeitig verwandte Wald- und Steppenformen aussterben? In einem Biotop wird es jedesmal Überlebende geben.

Warum sollen die jetzigen Waldarten, die nahe mit Steppenarten verwandt sind, erst kurze Zeit existieren? HANS STEINER (1952) hat für *Spermestes* Einwanderung im Mittel-Miozän, also vor etwa 20 Millionen Jahren, angenommen. Vier Arten haben sich natürlich seitdem entwickeln können. Ich stimme STEINER gern zu. Wenn die Gabelung zweimal erfolgen muss, so könnte die erste gut vor 16 Millionen Jahren erfolgt sein, also in einer Zeit, in der Afrika durch das Meer isoliert war. Die Aufteilung bis zu 8 heutigen *Malimbus*-Arten im Niederungswaldbereich führt uns auf sicher 3 Gabelungen nacheinander und damit etwa 24 Millionen Jahre zurück. Ich neige zur Annahme langer Gabelungszeiten, weil ich glaube, dass in letzter Zeit viel von kurzen Zeiten die Rede war, auch in der Paläarktis, und die Entstehung besonderer Unterfamilien, Familien, ja, einer Ordnung in Afrika spricht auch für lange Zeiten. Vielleicht ist es nützlich, einmal die Entwicklung der afrikanischen Vogelwelt als langsamen Prozess darzustellen. Bei schneller Entwicklung ergäbe sich nämlich gleich die Notwendigkeit, mehrere heute verschwundene Faunen und (oder) eine noch grössere Artenarmut des Tertiärs anzunehmen, als wir es gleich tun werden.

Die Zeit, die LÖNNBERG (1925) zum Differenzieren der afrikanischen Steppentiere zur Verfügung stellte, vom Pliozän bis heute, ist m. E. viel zu kurz. Der Grundstock auch der afrikanischen Steppenvogelwelt muss früher nach Afrika gekommen sein. Aber wann?

Die Isolierung durch die Tethys von der späten Kreide bis zum Miozän, von, sagen wir, vor 80 bis vor 12 Millionen Jahren, hat Afrika zwar im wesentlichen auf sich selbst gestellt, aber doch nicht ganz. Wie heute Ausbreitungen übers Meer hinweg erfolgen, so wohl auch damals, wenigstens vom Eozän an, als die Vögel sicher gut fliegen konnten und die heutigen Unterordnungen wohl alle schon vorhanden waren.

Es fragt sich nun, wie gross muss der Artenreichtum Afrikas damals gewesen sein, um die heutige Zahl von rund 1700 in Afrika brütenden Arten zu erzeugen? Ich möchte nicht annehmen, dass damals, mitten im Eozän, vor 50 Millionen Jahren, viel mehr als 10—20 Vogelarten in Afrika lebten, von denen im Laufe der Zeit noch eine Anzahl ausgestorben sein wird. Im Oligozän dürfte durch Aufspaltung und Zuwanderung die Zahl auf 125 gestiegen sein, die vor 29 Millionen Jahren den Beginn des Miozäns erlebten. Aus diesen 125 Arten könnten bis heute 1,500 geworden sein, 12 mal so viel.

Die Zahl 1,500 ist geringer als die tatsächlich heute vorhandene, weil noch die Zuwanderung zu berücksichtigen ist. Welchen Anteil hat die Zuwanderung im Miozän gehabt, vor 12 Millionen Jahren, als sich der Waldgürtel Indiens weit genähert hatte und die Landbrücke nach Asien entstand? Damals brachte das Südwärtswandern des temperierten Klimagürtels wohl manchen Holarkten und Paläarkten nach Nordafrika und weiterhin nach Südafrika, ich denke z. B. an die Gattung *Emberiza*. Wüsten- und Steppenbiotope wurden nach Westen und Osten hin über das Rote Meer hinweg bereichert. Vom Walde Indiens wanderte *Pitta*, aus indischen Savan-

nen wanderten *Pycnonotus, Criniger, Coracina, Argya* u. a. ein. Es kamen Gattungen, die in Eurasien beheimatet sind und in Afrika nur wenig Vertreter haben.

Die meisten Gattungen Afrikas aber, die in Eurasien fehlen, dürften vor dieser Zeit in Afrika entstanden sein, eben aus dem erwähnten Grundstock von 125 Arten zum Beginn des Miozäns. Sie, meine Damen und Herren, werden diese Zeitdehnung und teilweise Vorverlagerung der Einwanderung vielleicht ablehnen. Es ergeben sich tatsächlich dauernd Zweifel, z. B. bei *Numida*. Sind die Vorfahren der fünf Perlhuhngattungen erst im Miozän gekommen oder viel früher? Für »früher» spricht ihre Verschiedenheit, für »später», dass sich *Numida meleagris* (L.) noch mit *Gallus* kreuzt. Wie lange höchstens können getrennte Wesen kreuzungsfähig bleiben? Unterfamilien von *Anseres* kreuzen sich auch miteinander, obwohl sie wohl lange getrennt sind.

Schätzen wir die Zahl der Einwanderer nach den Indien und Afrika gemeinsamen Gattungen auf 9 % der *Passeres*-Gattungen Afrikas (also die Hälfte der 18 % beiden Gebieten gemeinsamen, Moreau 1952, p. 895), so wären das immerhin 24 Gattungen. Es müssten also etwa 800—900 Passeresarten in Afrika entstanden sein. Insgesamt dürften sich etwa 1,500 heute noch lebende Vogelarten Afrikas aus Stämmen entwickelt haben, die wenigstens Ende des Oligozäns, vermutlich meist schon im Eozän, anwesend waren. Für ihre Vermehrung von 125 auf 1,500 Arten steht eine Zeit von 29 Millionen Jahren zur Verfügung. Wie ich an anderer Stelle ausführen werde, halte ich als durchschnittliche Teilungszeit von zwei Vogelarten 8 Millionen Jahre für eine annehmbare Durchschnittsgrösse. Damit wären vor 21 Millionen Jahren 250 Arten dagewesen, von denen 20 wieder ausgestorben sein mögen, und die Vermehrung ging durchschnittlich im gleichen Masse bis heute weiter. Ich möchte also folgendes annehmen: Die Artenzahl der Vögel Afrikas für Beginn des Miozäns betrug nur wenig über 100 Arten, deren Vermehrung auf heute 1,500 Arten durch Aufgabelung der einzelnen Arten in jeweils (durchschnittlich) 1.8 überlebende Arten nach jeweils 8 Millionen Jahren erfolgt sein dürfte. Ich trete also für lange Artbildungszeiten, besonders in ausgedehnten Kontinenten, ein.

Zusammenfassung

1. Es wird vorgeschlagen, *Chloropetella* mit *Erythrocercus* zu vereinigen. Obwohl die äusseren Unterschiede dieser Formen und die der 20 *Pteronistes afer*-Rassen erheblich sind, ist es schwierig, Sicheres über räumliche Schranken zur Formbildungszeit auszusagen.

2. Etwa 16 % aller 1,700 afrikanischen Brutvogelarten, d. h. 70 % aller weit verbreiteten Arten, sind nach dem Typ der Savannenringe (um den Guinea-Urwald) verbreitet, zum Teil mit Einschluss des Urwaldes selbst.

3. Es besteht die Tendenz der Familien und Gattungen, zu sehen an der heutigen Verbreitung von etwa 75 % der 122 4 und mehr Arten enthaltenden (von 528 über-

haupt in Afrika brütenden) Gattungen, mehrere der Biome Niederungswald, Savanne, Wüste und Bergwald einzunehmen.

4. Die historische Entwicklung dieser Pluripotenz fordert nach Ansicht des Verfassers lange Zeiträume für die Arten- und Gattungsaufgabelung, vielleicht die durchschnittliche Aufgabelungszeit für zwei Arten von etwa 8 Millionen Jahren. Trotzdem ergibt sich eine schnelle Abnahme der Artenzahl bei einer Reise in die Vergangenheit: Die Artenzahl afrikanischer Vögel scheint im Eozän, vor 50 Millionen Jahren, 10—20 Arten kaum überschritten zu haben, wuchs vielleicht bis zum Ende des Oligozäns, vor 29 Millionen Jahren, auf 125 und bis heute auf 1,500 Arten, wozu noch die (200?) Nachkommen der wohl immer wieder und besonders in den letzten 12 Millionen Jahren aus Vorderasien oder Indien eingewanderten Vögel kommen.

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Zur Physiologie der Zugunruhe nächtlich ziehender Kleinvögel: eine Arbeitshypothese

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Putzig bezeichnet 1938 den Vogelzug sehr richtig als einen dynamischen, nicht statischen Vorgang. Das Auftreten des Wandertriebes — und ich meine, dass wir genügend Beweise dafür haben, die Zugunruhe gefangener, nächtlich ziehender Kleinvögel mit diesem gleichsetzen zu dürfen — ist sichtlich in ein jahresperiodisches Geschehen im Vogelorganismus eingebaut und muss deshalb meiner Ansicht nach auch unter Berücksichtigung desselben untersucht werden.

Hält man Dorngrasmücken *(Sylvia communis)* und Rotkehlchen *(Erithacus rubecula)* unter der Einwirkung der natürlichen Photoperiodizität (Frankfurt/Main) und kontrolliert dauernd die Motilität und das Körpergewicht, so stellt sich heraus, dass die dabei beobachtete Periodizität auch in aufeinander folgenden Jahren der Gefangenschaft (einzelne Tiere wurden bis zu 5 Jahren untersucht) immer die gleiche ist. Selbst individuelle Eigenheiten der Tiere bleiben überraschend konstant. Neben den erwähnten Dauerkontrollen bestimmte ich, meist für die Dauer von 1—2 Jahren, die Futteraufnahme und die Kloakaltemperatur (besonders während der Hellzeit). Der Gasstoffwechsel wurde in 42 stündigen, über das ganze Jahr verteilten Versuchen gemessen, in denen die Tiere ebenfalls etwa der natürlichen Photoperiodizität ausgesetzt waren und Futter aufnehmen konnten. Weiterhin versuchte ich, die aufgefundene Periodik durch Hormone und veränderte Umweltfaktoren zu beeinflussen. Die Ergebnisse sind in 3 Arbeiten niedergelegt. Sie seien hier kurz zusammengefasst, wobei ich allerdings aus Zeitmangel nur die Verhältnisse schildern möchte, die ich immer wieder bei einem bestimmten Typ von Dorngrasmücken, den ich den »schweren» nannte, feststellen konnte. Er war häufiger zu beobachten als ein anderer, der »leichte» Typ. Dieser zeigt Besonderheiten, deren Ursachen noch nicht geklärt sind. Die Rotkehlchen wiederum weichen in ihrem Verhalten von beiden Dorngrasmückentypen ab. Da sich in allen Fällen Übergänge finden, dürfte es sich um keine grundsätzlichen Unterschiede handeln, sie mögen vielmehr auf verschiedenen Reaktionsschwellen der Tiere beruhen.

1. Das Auftreten der Zugunruhe in Gefangenschaft stimmt zeitlich in wesentlichen Zügen mit dem der Freiheit überein. Ein Unterschied ergibt sich während der

natürlichen Brutzeit. In dieser besteht bei den gefangenen Tieren die Zugunruhe fort. Sie kommt aber sofort zum Erlöschen, wenn die Vögel stärker als gewöhnlich in die Fortpflanzungsstimmung kommen (sehr intensiver Gesang, bzw. Eiablage). Die gleiche Wirkung haben Sexualhormone (WAGNER, 1958).

2. Einige Zeit vor Beginn der Zugphasen kommt es, ausgehend von den Mittagsstunden zu einer sich immer stärker ausbreitenden Inaktivierung der Tiere in der Hellzeit (Sattelform der Verteilungskurve). Setzt die nächtliche Zugunruhe ein, sitzen die Vögel ab 10, 11 Uhr sehr häufig träge in den Futterhäusern, schlafen und fressen abwechselnd. Ausserhalb der Zugzeiten sind die Vögel entweder, wie im winterlichen Kurztag, während der Hellzeit gleichmässig aktiv oder sie zeigen, wenigstens in den Abendstunden einen hohen Bewegungsdrang. Im Tagesdurchschnitt findet sich die geringste Aktivität im Winter, der sich so als eine echte Ruheperiode zeigt.

3. Der Vogel in Zugdisposition oder Zugphase baut während der Hellzeit, synchron mit der Absenkung der Aktivität in hohem Masse Kohlehydrate in Fette um. Kurz vor Einsatz der nächtlichen Zugunruhe kommt es dadurch zu einer sprunghaften Erhöhung des Körpergewichtes. Dieser Vorgang wird durch eine Hyperphagie unterstützt, aber nicht ausgelöst. Das ergibt sich daraus, dass der RQ in jener Zeit auch dann über 1 steigt, wenn der Vogel verhältnismässig wenig gefressen hat. In den Zugruhephasen dagegen erreicht er höchstens für ganz kurze Zeit den Wert 1, selbst wenn der Vogel wesentlich mehr gefressen hat.

4. Die Bildung der Fettdepots muss demnach auf eine endokrine Umstellung — Einschaltung einer Sparregulation in der Hellzeit — zurückgeführt werden. In ihrem Gefolge sinken auch die Kloakaltemperaturen der Hellzeit und anscheinend auch der Blutzuckerspiegel (die Untersuchungen an Freilandvögeln sind noch nicht ganz abgeschlossen).

5. Der Ruheumsatz zugunruhiger Vögel liess sich nicht exakt feststellen, da sie fast den ganzen 24-Stundentag über kaum zu einer echten Ruhe kommen. Es ergeben sich jedoch keine Hinweise dafür, dass er absinkt und damit wesentliche Voraussetzungen für die Depotbildung schafft. Der Ruheumsatz liegt im Sommer höher als im Winter, worin sich dieser wiederum als Ruheperiode erweist.

6. Auf Grund der Motilitätsmessungen hat man den Eindruck, als ob die Aktivität der Vögel durch die Sparregulation der Hellzeit immer stärker auf die Nacht abgedrängt wird, in der sie sich dann voll entfaltet.

7. Der Nachtzug bringt für den Vogel sicherlich eine Reihe energetischer Vorteile. Die am Tage aufgebauten Fettdepots stellen bei geringst möglicher Gewichtsbelastung das Energieäquivalent für den Energieverbrauch der Zugunruhe. Dem natürlichen Tagesrhythmus des Vogels entsprechend liegen die Kloakaltemperaturen in der Nacht wesentlich tiefer als in der Hellzeit. Wenn auch noch zu klären ist, wie sich dazu die Korntemperaturen verhalten, so dürfte damit in jedem Falle eine Energieersparnis verbunden sein. Weiterhin ist die stark ins Gewicht fallende Nahrung bis zum Einsatz der Zugunruhe in der Hauptsache verdaut, bzw. ausgeschie-

den. Schliesslich steht dem Vogel die Hellzeit auf diese Weise voll zur Nahrungsaufnahme zur Verfügung.

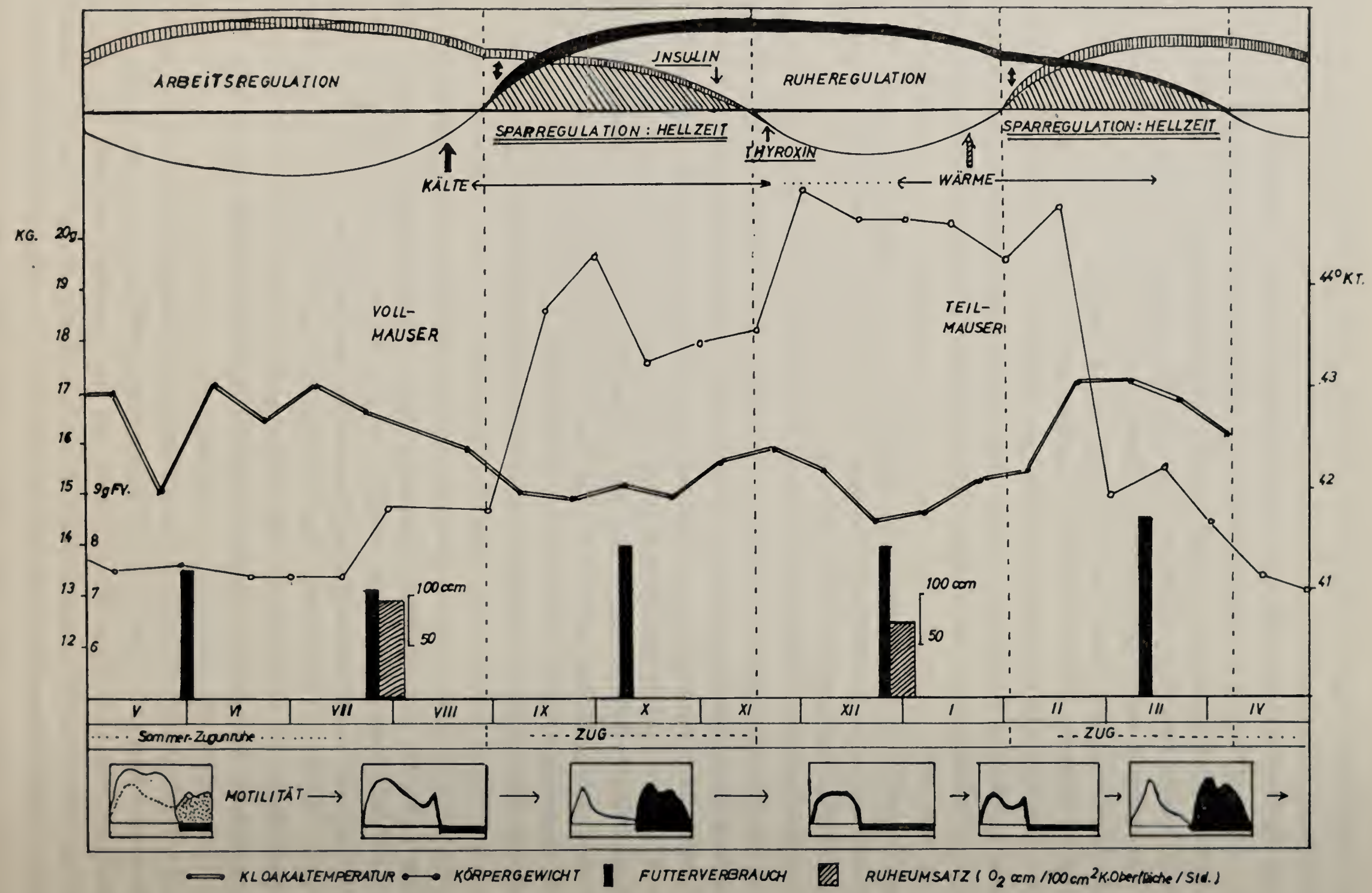
8. Meine Ergebnisse führen zu dem Schluss, dass eine verschiedene Ausnützung der Leistungsenergie im wesentlichen die Ursache für die Depotbildung in den Zugphasen ist. Demnach kann eine Messung der Energieaufnahme und die Bestimmung des Ruheumsatzes allein zu keinen befriedigenden Ergebnissen führen.

Diese in grossen Zügen zusammengefassten Befunde führten mich zu einer Arbeitshypothese, die ich an Hand der Abbildung S. 510 darstellen möchte. Die Kurven des Körpergewichtes (KG) und der Kloakaltemperatur (KT) stammen von einer bestimmten »schweren» Dorngrasmücke (D 19). Ich wählte das Beispiel eines bestimmten Tieres, da sich so Einzelheiten besser als an Mittelwertkurven aufzeigen lassen. Die schwarzen Diagramme verzeichnen den Futterverbrauch des gleichen Tieres, allerdings von einem anderen Jahre, die schraffierten Diagramme den mittleren Ruheumsatz von 4 Dorngrasmücken im Juli/August bzw. Dezember/Januar. Die Einzelbilder unten geben die für die Jahreszeiten charakteristische Verteilung und Höhe der Motilität etwas schematisiert wieder.

In der Zeit der sichtbaren Vollmauser im Juli beginnt das KG etwas zu steigen. Kurz vor und zu Beginn der Zugunruhe im September kommt es dann zu dem stärksten Gewichtsanstieg des ganzen Jahres. Erreicht die Zugunruhe ihren Höhepunkt, so übertrifft der nächtliche Energieverbrauch zeitweise die Energieeinnahme, und das KG fällt. Bald kommt es jedoch zu einem Ausgleich und für den Rest der Zugzeit pendelt das KG von Tag zu Tag um eine mittlere Höhe. Das Ende der Zugunruhe lässt sich auch an dem wieder ansteigenden Gewicht ablesen, das bald das Jahreshöchstgewicht erreicht. Die KT sinkt ab Juli in der Hellzeit gleichmässig ab, bleibt während der Zugphase auf gleicher Höhe und steigt gegen deren Ende wieder etwas an, ein Zeichen, dass die Sparregulation der Hellzeit beendet wird.

In den Wintermonaten Dezember/Januar behalten die »schweren» Dorngrasmücken das gegen Ende der Zugzeit erreichte hohe KG ungefähr bei. Die Aktivität der Hellzeit ist gleichmässig verteilt und pro Std. etwas höher als in der Herbstzugphase. Auf den 24-Stundentag bezogen ist die Motilität jedoch die tiefste des Jahres. Die kurze Hellzeit wird zur Futteraufnahme voll ausgenutzt. Die Kloakaltemperaturen der Hellzeit sowie der Ruheumsatz sinken auf die niedrigsten Werte des ganzen Jahres ab. Der Vogel hat somit eine Ruheregulation eingestellt, die ihm das Beibehalten des hohen KG ermöglicht.

Ab Februar nimmt die gesamte Aktivität des Tieres wieder zu. Eine schwache Teilmauser tritt auf. Der in den Mittagsstunden wieder über 1 steigende RQ, die Sattelform der Verteilung der Motilität und das erneute Ansteigen des KG zeigen an, dass die Sparregulation der Hellzeit wieder auftritt. Bald ist auch die erste Zugnacht zu beobachten. Obwohl der Futterverbrauch dieser Zeit der höchste des ganzen Jahres ist, gelingt es den Vögeln nicht, ihr hohes KG aufrecht zu erhalten. Die KT steigt an, und leiser Gesang tritt auf. Die Gonadenreifung beginnt. All das führt im Verein mit dem Energieverbrauch für die nächtliche Zugunruhe dazu, dass das KG


ARBEITSREGULATION
INSULIN
RUHEREGULATION
SPARREGULATION : HELLZEIT
THYROXIN
SPARREGULATION : HELLZEIT
KÄLTE
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KG.
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XII
I
II
III
IV
Sommer-Zugunruhe
ZUG
ZUG
MOTILITÄT
KLOAKALTEMPERATUR
KÖRPERGEWICHT
FUTTERVERBRAUCH
RUHEUMSATZ (O_2 ccm /100 cm^2 K.Oberfläche / Std.)

immer stärker abfällt. Mit dem Erreichen des Brutplatzes ist das KG auf dem Tiefstpunkt des Jahres angekommen. In der Gefangenschaft wird dieses Stadium meist nicht ganz erreicht. Das KG bleibt um etwa 1 g höher als das des Freiheitsvogels, der in Gefangenschaft überführt sein Gewicht im Ablauf von 14 Tagen um den gleichen Betrag erhöht und dann wie die schon länger gehaltenen Vögel ebenfalls in die Sommerzugunruhe kommt.

Das in der Abb. oben dargestellte Schema versucht eine Modellvorstellung von den Regulationsvorgängen zu entwerfen, die zu den beschriebenen Verhaltensweisen des Vogels im Jahreszyklus führen. Eine überwiegend ergotrope Faktorengruppe bestimmt im Sommer die Einstellung einer Arbeitsregulation, eine überwiegend trophotrope im Winter die einer Ruheregulation, die durch eine inaktive Schilddrüse charakterisiert ist. Im Verlaufe der Übergänge von einer Regulation zur anderen kommt es im Herbst und Frühjahr zur Ausbildung der Sparregulation in der Hellzeit, die zur Depotbildung und zur nächtlichen Zugunruhe führt. Diesen Vorstellungen entsprechen die Befunde, die mit Hormoninjektionen gemacht wurden. Thyroxin und Thyreotropes Hormon wirken besonders nach Ende der Zugzeit im Herbst und vor Beginn der Zugunruhe im Frühjahr zugauslösend, grössere Dosen vermögen es auch im Mittwinter. Sie verstärken die in der Ruheregulation des Winters stark zurückgetretene ergotrope Faktorengruppe und stellen damit entweder die Verhältnisse wieder her, die kurz vorher zur Herbstzugzeit bestanden bzw. schalten vorzeitig die Regulationsverhältnisse des Frühjahrs ein. Zu hohe Dosen dieser Hormone führen zu allen Jahreszeiten zu einer Regulation, die der des Sommers ähnelt und die Mauser auslöst. Insulin dagegen verstärkt die trophotropen Faktoren, senkt den Blutzuckerspiegel und schaltet damit vorhandene Zugunruhe aus. Nach grösseren Dosen beobachtete ich eine allgemeine Lethargie der Tiere, wie sie hin und wieder auch im Winter auftritt. Verabfolgt man in dieser Zeit Insulin, so führt das zu winterschlafähnlichen Zuständen, die tagelang anhalten können.

Mit der gleichen Modellvorstellung kommen wir auch zu Erklärungsmöglichkeiten für die festgestellte unterschiedliche Beeinflussbarkeit der Zugunruhe durch die Umwelttemperaturen im Herbst und Frühjahr.

Wenn man die Dorngrasmücke in eine der von Weigold bzw. Putzig aufgestellten Zugvogelkategorien einordnen wollte, so müsste man sie zu den Instinkt- oder innenweltbedingten Zugvögeln zählen. Die in allen Gefangenschaftsjahren gleichbleibende Periodik der Vögel führte mich zunächst zu der Annahme, dass endogene Faktoren dafür verantwortlich zu machen sind. In Abänderung der Versuche von Wolfson hielt ich von jeder der beiden Arten 10 Tiere vom Sommerlangtag ab dauernd künstlich in diesem: 6 Stunden Dunkelzeit, früh und abends je 50 Min. gut nachgeahmte bürgerliche Dämmerung und 16 Stunden Hellzeit. Die Versuche liefen bei Rotkehlchen fast 2 Jahre, bei den Dorngrasmücken etwas über ein Jahr. Untersucht wurden, zumindestens in Stichproben, die gleichen Faktoren wie bei den im Normaltag gehaltenen Tieren. Obwohl eine genaue Auswertung noch aussteht, lässt sich jedoch schon eindeutig feststellen, dass alle Tiere etwa in dem Zustande

verharrten, den sie normal im Juli erreichen. Der Gesang fiel fast völlig aus, Kleingefiedermauser trat häufig und völlig unregelmässig auf. Die Zugunruhe blieb bei den Dorngrasmücken abgeschwächt bestehen und wurde nur durch die Mauser kurzfristig unterbrochen. Bei den Rotkehlchen hörte sie schliesslich ganz auf. Die im Normallicht gefundene charakteristische Gewichtsperiodik verschwand, und das Gewicht pendelte um einen tief liegenden Mittelwert. Demnach steuert die Photoperiodizität auch das Verhalten von Dorngrasmücken und Rotkehlchen, endogen ist nur ihre Reaktionsnorm.

Im Winter ist der Südrand der Sahara die nördliche Verbreitungsgrenze der Dorngrasmücken. Das Überwinterungsgebiet erstreckt sich bis Südrhodesien und Damaraland, die südlich des Äquators liegen. Meine Versuchstiere lebten dagegen im Winter in der für sie unnatürlichen Photoperiodizität von Frankfurt am Main. Trotzdem fällt der Beginn der Zugunruhe im Frühjahr in eine Zeit, die etwa mit der übereinstimmt, in der sie auch in der Freiheit ihren Rückzug antreten dürften. Einige Rotkehlchen, die erst im Herbst, nachdem sie also schon einem erheblich kürzeren Tage ausgesetzt waren, zu den schon seit dem 21. Juni im Langtag verweilenden Rotkehlchen gesetzt wurden, zeigten im Gegensatz zu diesen im Frühjahr normale Zugunruhe. Dies könnte darauf hindeuten, dass der kürzer werdende Tag im Herbst den Anstoss für den Regulationsablauf bis zum nächsten Frühjahr gibt.

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Adaptation of Breeding Schedule to Latitude

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In approaching the subject of birds' responses to latitude, we may first recall and stress the fact that as a class birds are eye-minded and eye-controlled. Even among the nocturnal and crepuscular groups, the eye and the light stimuli are dominant in the activity of each species; the limited visual powers of the kiwis do not invalidate this generalization. It is a natural correlate of this circumstance that photoperiods and a certain range of light intensities are responded to in some way by all birds. Observation and experimentation invariably have shown reaction to light when tests have been critical, and we may assume that all birds will react, even though the proximate factor in the wild that regulates the schedule of a given species may be something other than light.

Breeding seasons in respect to their duration and schedule obviously must be highly adaptive. They are at the root of species reproduction, and in their evolution the selective pressures are compelling and direct to produce strong and sufficiently numerous young and to do so without waste of energy and individuals.

The one global regularity controlling the seasonal environment of all animals is latitudinal position and with it the corresponding light phenomena. An important part of the latitudinal light environment is the variation in length of the photoperiod, and because of the aforementioned impress of light on bird activity, essentially every species of the group must adjust to it, either adapting especially to the photoperiodism of its latitude or overriding its effect in adapting to something else more compelling. Seasonality in photoperiod ranges from none (constant day length of 12 hours, sun-up to sunset) at the equator to the extreme at or beyond the arctic and antarctic circles where continuous sun exposure or none at all prevails according to time of year. Birds will then be controlled seasonally by photoperiodism in more and more restrictive fashion with increase in latitude. It is this range of adjustment, from the equatorial situation to the arctic photoperiods, that I propose to examine particularly on this occasion.

At the equatorial extreme, where day length is a constant for biological purposes, it is my preliminary conclusion, based on current field work in Colombia, that the

slight seasonal changes in sun position and the minor variations in maximum light intensities are negligible as influences on birds. Moreover, the slight variation in photoperiod between latitudes 5° N and 5° S permits the recognition of other factors and adaptations and adjustments in seasonality. The more important of these are as follows, the source material being drawn largely from the group of papers on »Factors Determining the Breeding Seasons of Birds» (Ibis, 1950) by THOMSON, SKUTCH, MOREAU, LACK, and VOOUS:

1. Year-around breeding of species, or aseasonality, in breeding, is a condition far rarer at the equator than might be supposed. VOOUS (1950) was able to cite for equatorial Indonesia only a very few species which nest in all months or nearly all months of the year and even these showed seasonal peaks in amount of nesting, with the exception of two — *Lonchura punctulata* and *Lonchura leucogaster*. LACK (1950), reporting on the equatorial Galápagos Archipelago, noted that only certain of the sea birds nested throughout the year. MOREAU (1950), in covering equatorial Africa, submerged species data in favor of his analysis of faunistic or ecologic groups and their seasons as groups. Still it is fairly evident that there too only a few species at the equator breed continuously, and even those that do probably have peaks in breeding participation. Later (MILLER, 1955 b), I was able to show in equatorial South America that in a peculiarly constant, arid, or semiarid environment, with only weak manisfestation of wet seasons, 8 of the 10 species especially studied were in breeding condition at all periods of the year. However 4 of the 8 probably were more abundantly in breeding state at given periods than at others. The conclusion derived from these general findings is that year-around breeding, although permissive from the standpoint of constant adequate photoperiods, is usually warped or definitely ordered by adaptations to other variables.

2. In species that breed at all periods of the year or which show no more than seasonal peaks in a continual breeding performance, the breeding participation of the individual may largely reflect the innate rhythmic tendency of the species. Thus in my earlier study (MILLER, 1955 b) of Colombian birds some evidence and reasons were adduced for passerines to suggest a 6- to 8-month total cycle in any one individual. A more thorough check of marked individuals of known breeding history needed to be undertaken and is currently being attempted with *Zonotrichia capensis* which as a species shows at least some breeding the year around. Already some short histories of a few males indicate that the quiescent period with reduced testes is in the order of only one month, but it remains to be seen whether there is maximum development over the remainder of a 12-month span or another recession in 6 or 7 months. In the Sooty Tern *(Sterna fuscata)*, CHAPIN's (1954) data on breeding reflect a $9\,{}^{3}/_{5}$-month innate cycle since no environmental variable has this periodicity.

3. Environmental adaptations at the equator to factors other than light are the rule and center chiefly in seasonal variation in rainfall. These adaptations, *per se*, really fall beyond the scope of this paper except as they show the release

from the otherwise compelling control by light. CHAPIN (1932: 54) has reviewed, for within 5 degrees of the equator, the basic geographic data (after MARTONNE) which indicate a tendency for two dry seasons, one in December and January, the other in June and July, the latter less pronounced north of the equator, the former less pronounced south of the equator. MOREAU presents (1950: 226) a rather similar picture and his as well as CHAPIN's reviews (1932: *op. cit.*) of relations of breeding to wet and dry seasons in Africa apply broadly to other equatorial areas as follows. Briefly, we find all manner of individual species adjustments to breeding so that species may nest either in the wet or dry seasons or at the beginning or ending of them. The responses are so varied, species by species, and according to ecologic type and local climatic belt that the effect of wet and dry periods tends to be minimized, but for each species it is my feeling that it is a very real adaptation. The proximate factors or stimuli that make this scheduling possible are equally variable and often must be some element other than the fall of rain itself, as the attainment of breeding readiness frequently proceeds far before the onset of rain. MOREAU properly brings out such possible proximate factors as vegetation changes affecting food supply, mere visual stimulation by the change of appearance of vegetation, the stimulus of showers in advance of periods of significant rainfall, and the perception of humidity as such. Recent experiments by MARSHALL and DISNEY (1957) show the influence of seasonal availability of suitable nest materials. But the point to stress is that all these devices seem but mechanisms for attaining proper coincidence of breeding readiness and the appropriate wet or dry period when the particular species can most successfully nest and in which its young can most effectively be nourished.

4. A special type of adaptation at low or moderate latitudes, independent of photoperiodism, is that of quick response in very arid regions to onset of rains which may come at irregular and long intervals. This situation is especially well shown in interior Australia. The main feature of this desert adaptation appears to be ability to respond rapidly, either holding a state of breeding readiness or attaining it in a matter of a relatively small number of days, so that breeding can coincide with the rains or their immediate, desirable after-effects.

5. Temperature as a factor at the equator probably promotes few direct adaptations independent of the rainy season although there may be some. VOOUS (1950) and MILLER (1955 b) both found insignificant temperature fluctuations within 5 degrees of the equator, and no one so far as I am aware has yet shown a primary adjustment to either the high or low temperature peaks, slight in amplitude as they are, at these latitudes.

6. CHAPIN's Sooty Terns, already referred to as reflecting an innate $9\,^3/_5$-month rhythm at Ascencion Island, nonetheless must respond to some factor which holds the whole colony in synchrony, otherwise the natural individual variability of the $9\,^3/_5$-month cycle would soon lead to a situation wherein there would be breeding, for the species, in all parts of the year. The factor is apparently a social stimulus

— the Fraser Darling effect — to which the species is bound and which dictates breeding in large colonies stimulated by sight of others gathering, courting, and nesting. Deviations in innate rhythmic tendency are thus coerced to conform as a social adaptation, since all physical environmental factors are such as to permit breeding at any time. MARSHALL and DISNEY's (1957) experiments on *Quelea quelea* point also to the role of social stimulation, among other factors, in modifying the expression of internal rhythm.

The arctic latitudes, basically because of the seasonal sun cycle, obviously require rigorous scheduling of the breeding season. Nesting can usually entail only one full brood effort at the arctic circle, so that the breeding season is short. In passerines, full breeding capacity of males is seldom sustained for more than 4 to 6 weeks. Moreover, the coordination of individuals within a population is impressive. Usually the variation in attainment of a particular stage in territorial establishment, nest-building, or laying spans but a week to 10 days in a given species as OAKESON (1954) and PITELKA's studies (1957; fig. 8) in high latitudes in Alaska have well shown.

Full reproductive capacity must be reached somewhat in advance of actual need in order to insure readiness and adjustment to year to year variables in weather and melting of snow cover. The proximate stimulus of this recrudescence in males must be chiefly some aspect of photoperiod, either early or mid-way in the stages of recrudescence, else the regularity in preparation could not be so tightly scheduled and coordinated within the species. This fundamental contention, originally developed and in part tested so admirably by ROWAN (1929), must I believe stand generally valid for high latitude populations.

Recently, PITELKA (1958) has shown that in resident species and also in migratory species in which molt occurs before the southward flight the limited arctic summer period must accommodate not only the breeding activity but the perhaps equally energy-demanding new annual feather growth for all members of the population. The adaptation to the food flux of the arctic summer and the neat way of utilizing it in the two potentially competing functions of reproduction and molt by proper spacing and timing brings new understanding of the rigors of adaptations and requirements in the arctic.

One facet of the arctic adaptation, perhaps little thought about, yet one which becomes impressive after study of equatorial groups, is the energy-saving aspect of the long annual quiescent period of the gonads. Many equatorial species have partly or totally enlarged gonads for many months of the year during part of which time they are not nesting or are at most undertaking new nesting on a very leisurely schedule with many long intervals between stages of the process. To maintain the gonad tissues at full size and to sustain much of the activity which their sex hormones stimulate apart from actual nesting constitutes a large energy drain. This energy is saved in high-latitude species, adaptively, for applicability to migration or winter cold resistance, or for mere conservation of the food intake and the ecologic food

resources in their winter or migratory-route environments. The quiescent period in the pituitary-gonad cycle, which seemingly all wild species experience, is to be thought of as adaptively prolonged. The bird for a time »resists» light stimuli at latitudes where it has arrived to winter. Or, later in the year, a higher threshold is set for photoperiod stimulation than in southerly resident forms, both in order to conserve energy and to set the schedule of recrudescence and/or migration sufficiently late so as to be adaptive to the conditions of late-developing spring on the nesting grounds.

The problem that particularly confronts all considerations of adaptations of a functional kind is the obtaining of evidence that the differing physiologic responses have a heritable basis and are not merely labile adjustments in a general and widespread physiologic process. Unless innate differences are demonstrated, we really have no right to consider the seeming modifications of breeding season to latitude as evolutionary changes or adaptations in the proper sense. The evidence for heritable differences in physiologic response is difficult to obtain but probably may most significantly be sought in closely related forms that have a considerable latitudinal range and consequent adjustment. The genus *Zonotrichia* in North America, and especially *Zonotrichia leucophrys* of the Pacific seaboard, offers such an opportunity.

In *Zonotrichia leucophrys* there is a series of physiologic races which, although their attributes have not been tested in cross-breeding, have been observed and tested experimentally in such a way as to show that they possess stable and consistent differences of response which are not reversed or altered by holding the birds under abnormal conditions or by holding the several types under identical conditions. These attributes thus may be presumed to be innate. Especially is this true when differential responses are found among young birds of the different races and latitudes which have had no previous breeding cycle and thus no opportunity for any environmental conditioning that might otherwise be thought to explain some of the differences in breeding physiology displayed. These comparative experimental studies, which were earlier begun by Wolfson (1945), are now being pursued independently by Farner and me, with results that are generally confirmatory. This work is based on underlying observational and histological studies, chiefly those of Blanchard (1941).

The breeding range of the populations of *Zonotrichia leucophrys* extends continuously from latitude 35 to latitude 67 above the arctic circle and encompasses three color races useful in identifying winter-taken examples. The races are *nuttalli* of coastal California, which is non-migrant, *pugetensis* that breeds on the coast of Oregon and Washington, primarily, and *gambelii* of the mountains of British Columbia and the western arctic taiga belt. A related species, *Zonotrichia coronata* (= *atricapilla*) occupies a similar latitudinal breeding range to *gambelii* but is restricted to the mountains and coastal western Alaska.

All four of these forms winter together at latitudes 35 to 40 degrees in central California, joining in common flocks in part, and utilizing similar brush cover along

the coast. Thus from October 1 to the time of the spring migration, they experience identical environment. Yet these wintering populations show differential response to photoperiodism, revealing innately different thresholds to vernal light increase. This is reflected by the time of attainment of full reproductive state (stage 7 of BLANCHARD) of the testis. This occurs in early March in *nuttalli*, mid-April in *pugetensis*, mid-May in *gambelii*, and late May in *coronata*. The differential within *Zonotrichia leucophrys* is thus a maximum of $2\,^1/_2$ months and it is 3 months within the whole complex (see fig. 1). When these same populations are subjected to artifi-

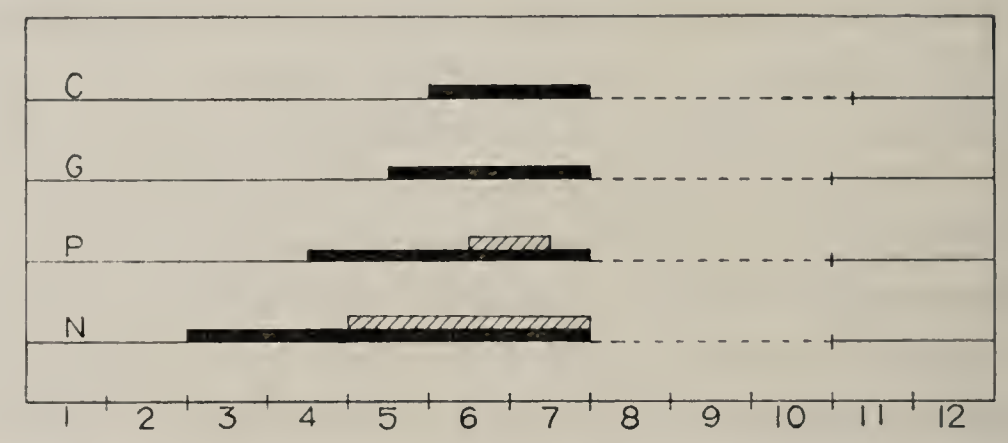

Fig. 1. Comparison of breeding seasons of forms of *Zonotrichia* on the Pacific coast of North America. C, *Zonotrichia coronata;* G, *Zonotrichia leucophrys gambelii;* P, *Z. l. pugetensis;* N, *Z. l. nuttalli*. Lengths of solid black bars represent span of breeding season (months shown on abscissa) in terms of full reproductive state of males. Cross-hatched bars represent span of breeding state in experiment in which vernal light stimulus was withheld; note that *coronata* and *gambelii* do not attain breeding state under these conditions. Broken lines represent postbreeding refractory period, the termination of which (experimentally verified in *coronata* and *pugetensis* only) is marked by vertical bar.

cial light stimulus in an experimental cage beginning in November with a 15-hour day, they respond differentially in the same way and sequence, although the differential between forms is somewhat shortened. Thus between *Zonotrichia coronata* and *Z. l. pugetensis*, the attainment of full reproductive state is separated by about 20 days instead of the 45 days that prevails both in the wild and in controls. Comparable shortening by half or more occurs for the other intervals. Therefore the experimental check of the differential response strongly indicates that a difference in threshold to light stimulus is the key physiologic adaptation of the latitudinally adjusted breeding seasons of these zonotrichias.

Not only do these zonotrichia populations initiate changes differentially in the spring, but they show a different length of the breeding plateau (fig. 1). Onset of refractoriness or regression is much the same in them in point of date, but the earlier beginning of the breeding state means an ability to sustain activity against possible light-induced refractoriness (see BURGER, 1953) in the southern populations, or conversely, in line with what was suggested earlier, an adaptive energy-saving refractoriness after a short breeding season among the northern populations. The end result in any event is a breeding season of males of 5 months in *nuttalli*. The season grades down to 2 months in *coronata*, and even this latter may be a little

longer than real. Moreover these sustained plateaus have the same duration in control birds held captive at latitude 38° in California as in the wild.

Another experimental procedure (MILLER, 1955 a) which reveals innate differences in light response and in internal rhythmic tendencies is the withholding of vernal light increase to determine the ability of the different forms to attain fully developed testis condition on the basis of their own tendency to recrudesce. Experimental birds are put on a light regime of the same length that they receive normally at the winter solstice in central California and they are then allowed no light increments thereafter. The differential results are spectacular. *Nuttalli* and *pugetensis* attain full reproduction state but both of them do so 7 or 8 weeks late compared each with its norm (fig. 1). Moreover *pugetensis* tends to shorten the season at the end under this limited light, although termination is irregular in both forms. The plateau in *nuttalli* is thus only of about 3 months duration rather than 5 months and in *pugetensis* it is but one month or less, rather than 3 $^1/_2$ months.

In *gambelii* and in *coronata* the birds never attain breeding condition. Individuals have been kept a full year in the case of *coronata* and two years in *gambelii*, and yet they have never shown any recrudescence. Thus in these forms the rhythmic tendencies, such as they may be, are inadequate to bring the birds to breeding state in the absence of vernal light stimulus. In other words they have evolved a physiologic system in which a vernal light stimulus is absolutely required whereas their relatives, although influenced by such light, are not fully dependent on it.

To view these adaptations in another way, we may, from what we know, stress how badly non-adaptive one form would be in the breeding range of another. For example *gambelii*, if staying in the breeding range of *nuttalli*, would, in view of the shorter days and its normally later start, probably have little more than a 2-month period of breeding potency while its competitor would have a 5-month period. Obviously *nuttalli* would out-produce it and better spread its food utilization while nesting over a period appropriate to the ecologic production of the middle latitudes. On the other hand, *nuttalli* on the range of *gambelii* would attain a breeding state, and indeed arrive there, some two months ahead of snow clearance and would, non-adaptively, fail to survive, fail in breeding effort, or at least experience great waste of energy by waiting in breeding readiness for the arrival of a late spring.

The progressive relaxation of the underlying photoperiod adaptation in an equatorial direction may be traced through the appearance of cyclic regimes that gradually depart in compromise adaptation to other aspects of the environment. Eventually a situation is reached where some species, although possibly still timed and influenced by the photoperiod, nonetheless have a schedule set to breed during the shortest days of the year (nocturnal owls are not considered in this connection). The relaxation appears at mid-latitudes and tends to involve more and more species from latitude 38° equatorially. We may cite a few examples. JOHNSTON (1954) has shown very nicely how the breeding seasons (first clutches) of Song Sparrows (*Melospiza melodia*) have their peaks earlier in the calendar year to the southward in

the great latitudinal spread of this species; this permits a longer breeding season with more broods farther south, at least as far as California on the west coast of North America. What is most significant, however, is the fact that first broods at latitude 38° in California in the San Francisco Bay region occur two weeks earlier in the salt marsh races (JOHNSTON, 1956) than in the local upland race, which latter conforms to the general latitudinal trend for the species. The salt marsh race has adapted, by whatever system of proximate stimuli we do not know, to nest earlier in its tidal habitat and avoid the period of especially high spring tides in late April which would destroy much of the nesting effort; a number of repeat nests in late April have been found actually to suffer severe loss. The same light environment, then, has permitted these two populations to diverge, the compelling need in the salt marsh habitat off-setting to a degree the general photoperiod adaptation of the species at the latitude concerned.

In southern Arizona and northern Chihuahua, from latitudes 30° to 32°, the Montezuma Quail *(Cyrtonyx montezumae)* is known to nest chiefly in late July. The peak of the hatching occurs on August 9 (LEOPOLD and MCCABE, 1957) whereas hatching periods of many species at these latitudes fall, more normally in terms of photoperiod, from April to June. The Montezuma Quail and some other species of this latitude and climatic belt adapt to the summer rainfall regime, which means hatching young at the beginning of the period of lush vegetation and insects which follows the onset of rain in July. Obviously at this latitude, where there is a rather severe inland type of winter at the upper elevations, such an adjustment could not violate the seasonal light and temperature situation completely, but there is a sufficiently prolonged mild autumn period that permits this special adaptation to utilize the benefits of the late summer rains. What is still unknown in the group of species that the Montezuma Quail exemplifies is whether a physiologic state of readiness is attained much earlier and held until finally triggered into action by the onset of rains. This has been suggested but I think it is doubtful, as the rains are fairly regular in their timing, unlike those of the Australian deserts, and to wait long in readiness would seem to be wasteful of energy.

The most striking adaptation contrary to latitude that I know of for a relatively far northern position is that of the Anna Hummingbird *(Calypte anna)* at latitudes 36° to 40° in central California. WILLIAMSON (1956) has recently assembled the most complete information on this species. This hummer attains reproductive state in males by progressive stages in October and November and by December it is in full reproductive state. Moreover, actual nesting begins then and takes place chiefly (first nests) in December, January, and February, a period encompassing the winter solstice and when there is only 10 hours of daylight at this latitude. Even late and repeat nestings cease by the end of May. The species has evidently adapted, despite the disadvantages of short winter days, to the wet season in California which follows the onset of late fall rains. The coastal belt has sufficiently mild temperatures to permit flowering of many plants in winter and very early spring. Nevertheless

somewhat inland I have seen this species at latitude 39° incubating eggs during a light snowfall in January. However the surrounding manzanita bushes were all in bloom.

One of the most interesting cases of modification of season in mid-latitudes, but one for which the data are imperfect as yet (MILLER, 1957: 379—381), is that of the Black-throated Sparrow *(Amphispiza bilineata)*. This is a desert species occupying the arid southwestern United States and the elevated central plateau of northern and central México. In general it occupies interior situations but it reaches the coast in arid Baja California and on the islands of the Gulf of California. Within this one species there is a complete reversal of a northern summer breeding period to one in which breeding occurs in the shortest days of the year, where, slightly farther south, this is evidently permissive. In general the species seems to nest when otherwise possible during or soon following the rainy season. However between latitudes 28° and 38° it breeds from April to June in the interior deserts regardless of rain. Any other period would entail nesting in the cold interior winter of these deserts or during the extreme summer heat, which heat is more pronounced because of longer days than farther south in Mexico. But between latitudes 20° and 26° in Baja California breeding condition and nesting occurs from October to June, during or following such slight rains as may fall, and on the central Mexican Plateau it occurs from June to September when the quite regular summer rains there set the breeding season. Thus the species in its range from latitude 20° to 38° may be found nesting in every month of the year, but at no one place for any extended span. The season is photoperiod-related in the north but is adapted otherwise in the south where photoperiod domination diminishes near the Tropic of Cancer.

Farther within the tropics, as MOREAU's (1950) and SKUTCH's (1950) reviews well bring out, the correlation with the light values of latitude weakens markedly, and many complex adjustments, chiefly to rainy season, occur, and there are many complex problems of proximate regulatory stimuli. Yet SKUTCH in his exhaustive experience with nesting seasons in Central America, chiefly in Costa Rica, within 10° N latitude, says (p. 221) that »the peak of the nesting season falls between the vernal equinox and the summer solstice, with April the principal month of laying . . . Relatively very few birds nest during the half of the year from September to February, inclusive.» This conclusion is derived from observation both in dry and humid belts of Central America. Thus at latitude 10° photoperiodic influences are clearly felt and probably these prevail weakly even to latitude 5°. Certainly they are far from absent at 8° in Panamá.

SUMMARY

Certain points of emphasis in this review paper may be restated. Adaptations of breeding physiology to latitude and photoperiod are abundant, and they are widely recognized and almost self-evident. Yet these adaptations are only imperfectly known in detail. The critical test of such adaptations lies in demonstrated heritable

physiologic differences among close relatives, namely races or populations of the same species or of closely related species. A case is cited in which some progress has been made in demonstrating such innate differences within the genus *Zonotrichia* on the Pacific coast of North America. Increased rigor of the requirements of photoperiod at progressively higher latitudes masks or minimizes other ecologic correlates. Ranging equatorially, on the other hand, at latitude 38°, adaptations of seasonality other than to photoperiod become clearly demonstrable, chiefly in reference to rainfall, and at latitude 26°, rarely even at 38°, some species may partly or completely overcome photoperiodic strictures in adapting to other factors. Yet at latitude 10°, and probably even at 5°, the influences of seasonal photoperiod *per se* are detectable in the majority of species.

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Some Adaptations Which Help to Promote Gregariousness

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INTRODUCTION

All birds show some tendencies toward gregariousness, at least in some circumstances or at some stages of their life cycle.

The term »gregariousness» is rather difficult to define precisely. It is frequently used in a very broad sense, to include all non-hostile and non-predatory reactions between two or more individuals, with the exception of sexual reactions between mates or potential mates and relations between parents and young. I shall, however, use the term in a somewhat more restricted sense in this paper, to include only the positive tendencies of birds to approach, join, or follow other birds (except mates, parents, or young) in a more or less peaceful manner.

The advantages, *i. e.* adaptive values, of gregariousness are probably numerous. They are obviously different in different species, and frequently different in the same species in different situations. I do not want to discuss this subject in detail here, except to note that gregarious habits may facilitate the discovery of, and escape from, predators, and/or the securing of suitable mates, and/or the discovery and most efficient utilization of food sources. The food factor may be the most important in the majority of extremely gregarious birds, as gregariousness seems to be particularly characteristic of insectivorous species, and birds whose food, such as fish or carrion or fruit, usually occurs in large irregularly scattered masses. (See Allee, 1958; Collias, 1950; Cott, 1946; Darling, 1952; Emlen, 1952; Friedmann, 1935; Rand, 1954; and Tinbergen, 1953; for some general comments on the distribution of gregarious habits among different orders and families of birds, and the probable usefulness of such habits in a wide variety of cases.)

In spite of the fact that gregariousness must be very advantageous in the lives of many species, it is seldom or never allowed free play without conflict or competition with other opposing or incompatible tendencies. Its expression is usually or always impeded to some extent, however slight, by the hostile or agonistic drives, *i. e.* attack and escape. Any approach by one bird toward another usually seems to activate the hostile drives of both. This hostility may be too weak to be expressed by overt, unmistakable, attack or escape movements; but its presence can usually

be detected by suitable analysis. It may, at least, be one of the causes of many ritualized social signal patterns or »displays» which tend to occur whenever one bird tries to approach another.

The term »display», in this sense, includes all vocalizations, and all movements and postures which have become specially adapted, in physical form or frequency, to subserve social signal functions.

The adaptive value of such hostility is not always evident at first sight. The widespread distribution of aggressive responses may be particularly difficult to understand; but the mere fact that such responses *are* so common, found in so many species in so many different circumstances, must indicate, I think, that they are definitely advantageous on the whole. (They must, in fact, be extremely advantageous in at least some situations, in order to compensate for the obvious disadvantages they must always entail, to a greater or lesser extent, in all situations, *i. e.* the risk of fighting and subsequent physical injuries and general interference with all sorts of useful and necessary social relations.) One presumes that the primary value of this hostility is its »spacing out» or dispersing effect, the prevention of undue crowding or concentration of individuals in restricted areas. And this effect, of course, may be advantageous for many different reasons in different species (see, for instance, ALLEE, *op. cit.*).

The fact that all or almost all reactions by one bird to another, even the most nearly completely »friendly» reactions, are apparently inevitably ambivalent would indicate that highly gregarious species have been confronted with a particularly difficult »problem» in the course of evolution. They have had to evolve methods of increasing or facilitating the general gregarious and flocking tendencies, and simultaneously controlling the hostile reactions which increased gregariousness would otherwise tend to aggravate.

Different species have attained either one or both objectives by evolving a variety of special sign stimuli and associated adaptive behavior patterns.

Some degree of gregariousness may well be primitive in birds (and vertebrates in general, for that matter); but the most extreme gregarious habits of some modern species are probably highly specialized. Extreme gregariousness is largely confined to a relatively few groups and species of modern birds, mostly species which are highly specialized in other ways as well.

SOME ADAPTATIONS TO PROMOTE GREGARIOUSNESS DIRECTLY

It may be convenient to consider the different types of adaptations designed to increase or facilitate gregariousness separately, beginning with some of the characters which seem to promote the general flocking tendencies directly.

Many of these »positive» adaptations are obvious and well-known; (see, for instance, COLLIAS, 1950 and 1952; COTT, *op. cit.;* EMLEN, *op. cit.;* LORENZ, 1931 and 1938; MOYNIHAN and HALL, 1954; and TINBERGEN, 1951 and 1953). They may be rather arbitrarily divided into morphological and ethological adaptations.

(1) Conspicuous coloration and »flash» patterns

Many of the more gregarious species of birds have evolved particularly conspicuous plumage colors and patterns, in either one or (more frequently) both sexes.

A very large proportion of such species, for example, are predominantly black (*e. g.* many corvines, many icterids and sturnids, anis, cormorants, cathartid vultures, etc.), or predominantly white (*e. g.* many herons, spoonbills, swans and some geese, some cotingas, etc.), or pied (*e. g.* magpies, many gulls, terns, and shorebirds, etc.).

The adaptive value of such coloration seems fairly clear. It will be generally advantageous for *any* species to be as conspicuous as possible, insofar as conspicuousness will make it easier for individuals to locate and recognize one another. It is also possible that conspicuousness may actually make a bird more »attractive» to its fellows; or even enable it to convey stronger and more effective sign stimuli for all sorts of social reactions. In most species, of course, these advantages are more or less counterbalanced by the fact that conspicuous individuals are more exposed to predators; but highly gregarious species are probably less vulnerable than less gregarious forms. Groups of birds can not only discover predators more efficiently than single birds, but can probably also defend themselves with greater chances of success. Highly gregarious species can thus »afford» to develop a greater measure of conspicuousness than less gregarious forms.

Another characteristic of many highly gregarious species is the development of »flash» colors and patterns on wings, rump, and/or tail; striking patterns of color, contrasting with the rest of the plumage, which are suddenly revealed or emphasized when a bird flies. They seem to be designed to stimulate the tendency, apparently present in almost all birds, to follow any other flying bird, especially any bird flying away. They certainly increase the visual conspicuousness of flying up movements (and the preparatory flying intention movements — see below).

Such colors and patterns have been given special names (*e. g.* »episematic» by Huxley, 1938, and »proepisematic» by Cott, 1946); but they are not confined to gregarious species alone, and similar characters may also subserve other functions. It should be noted that the types of conspicuous coloration which tend to promote gregariousness in some species are nearly identical with some types of conspicuous coloration subserving other, *e. g.* aposematic, functions in other species (see Cott, 1940). It is even possible that the conspicuous color patterns of some species may be both »attractive» to other members of the same species and »warning» to other species at the same time.

(2) Some calls and movements promoting gregariousness directly

Conspicuous and flash color patterns are usually complemented or supplemented by special ethological adaptations.

Many highly gregarious species are notoriously noisy, uttering loud notes (the

so-called »contact notes») almost continuously in many circumstances. This habit probably increases their general conspicuousness even more than striking coloration. Increased frequency of calling is perhaps most characteristic of small gregarious passerine birds, such as some formicariids (JOHNSON, 1954), tanagers (personal observation), ploceine finches (FRIEDMANN, 1950), and estrildine finches (MOYNIHAN and HALL, *op. cit.*, and M. F. HALL, personal communication). It is not hard to understand why this should be so. Gregarious small birds are probably more vulnerable to predation than gregarious large birds; and calling is a form of conspicuousness which can be easily »turned off» at will in case of emergency.

Flash patterns on wings, rump, and/or tail are often strictly correlated with more or less extreme flying intention movements. Many highly gregarious species have evolved exaggerated and obviously ritualized wing and/or tail movements, such as flicking, waving, drooping, quivering, etc. These are usually performed by any individual preparing to fly. They signal the intention of flying in a quite unmistakable manner; and thus facilitate or stimulate following by other individuals (see DAANJE, 1950, and ANDREW, 1956).

The widespread tendency of almost all birds to follow other birds in flight seems to be particularly important in maintaining the integration of flocks; and this may help to explain why some highly gregarious species have become unusually »restless» or mobile. The Plain-colored Tanager, *Tangara inornata*, a common Panamanian species which I have been able to observe at some length, may be cited as an example. Plain-colored Tanagers are highly gregarious, insofar as they almost always associate in small flocks; and their flocks are constantly on the move from place to place. A group of these tanagers, for instance, will often start to feed on the fruits of a particular tree (such as a *Cecropia*), continue feeding there for a few seconds, then fly off to a nearby tree of the same species whose fruits are in the same stage of development as those of the first tree, then fly back to the first tree and feed again on the same fruits as before, then fly to a third tree of the same species and begin to feed on more of the same essentially identical fruit, then fly back to the second tree for still more feeding, etc. — all in the space of less than two or three minutes. It is difficult or impossible to believe that all these moves are due to successive activations of several different feeding drives or other types of motivation (the birds may be very restless without giving any overt indications of activated hostile or reproductive drives). This restlessness may be adaptive because it counteracts the tendency toward dispersion which may occur if the birds continue to feed in the same tree for a long period of time. (As the original source of food becomes exhausted, the birds usually tend to diverge gradually in search of more food in other parts of the tree, if they are not interrupted and brought together again.) It is noticeable that the birds tend to »bunch» together whenever they fly off. The same tendency to come together during flight is present in many other less gregarious species as well; but the fact that Plain-colored Tanagers fly more frequently than less gregarious species means that they will come together more often.

The development of extreme gregarious habits is probably accompanied by important changes in the internal organization of different drives or types of motivation; but such changes are very difficult to analyze and have been very little studied. I will not, therefore, attempt to discuss their probable or possible nature in detail here; but it might be useful to recapitulate some brief and general comments on the subject which have already been published elsewhere (MOYNIHAN and HALL, *op. cit.*).

There has been some debate about the possible existence of a »general social» or gregarious drive or instinct. TINBERGEN (1951) suggested that there was no gregarious or social instinct as such (when the term »instinct» is defined as a »hierarchically organized nervous mechanism which is susceptible to certain priming, releasing and directing impulses of internal as well as external origin, and which responds to these impulses by co-ordinated movements that contribute to the maintenance of the individual and the species»). He suggested that the gregariousness of animals which exhibit this trait in some circumstances but not in others — and very few or no species are gregarious at all times — can be most simply explained by supposing that a variety of different instincts, *e. g.* feeding or sleeping, may have gregarious aspects (*i. e.* the presence of other animals may be part of the adequate stimulus situation when these other instincts are activated).

This may well be true in many cases; but there is also some evidence to indicate that at least a few of the most thoroughly gregarious birds, such as the Plain-colored Tanager and some estrildine finches, do have a general gregarious instinct which has become partly independent, in some sense, of all other instincts.

It is even possible that some of the highly gregarious species which are particularly restless in almost all circumstances may have developed some sort of partly independent »mobility drive» as well.

ADAPTATIONS DESIGNED TO PROMOTE INTER-SPECIFIC GREGARIOUSNESS

Most characters which are adapted to increase gregariousness directly have been evolved to promote intra-specific flocking tendencies; but some of them seem to have become adapted to attract or otherwise influence members of other species also, and some comparable characters would seem to have been evolved for this latter purpose alone.

Mixed flocks composed of several species are very common in some areas, (see, for instance, CHAPIN, 1932; DAVIS, 1946; MURPHY, 1936; ODUM, 1942; STANFORD, 1947; WING, 1946; WINTERBOTTOM, 1943 and 1949; and the extensive discussion in RAND, *op. cit.*).

Most of the species included in such mixed flocks may secure many of the same advantages that more exclusive species secure by flocking by themselves. (Many, but not all, species which tend to join mixed flocks in some circumstances will form flocks composed solely of their own species in other circumstances.)

The adaptive characters promoting the formation of mixed flocks, or resulting from the formation of such flocks, are much the same as those promoting or resulting from the gregariousness of a single species. This is certainly true of conspicuous coloration, for instance. Some of the color patterns of species which tend to join mixed flocks are particularly interesting, however, as they seem to be inter-specific signals of a rather peculiar kind.

(1) Social mimicry and similar phenomena

Two or more species with roughly similar habits, living in the same general environment in the same regions, and frequently associating with one another, may show remarkably similar signal patterns. This may be due to a variety of causes, and subserve a variety of functions, in different cases. Some of the similarities between different species in mixed flocks may be due to common descent. The species may be closely related, and have retained many of the characters of their common ancestor, or developed these characters along parallel lines. (Related species usually have roughly similar feeding habits; and this is probably one of the reasons that many mixed flocks are primarily composed of such species, *e. g.* the mixed flocks of titmice in northern woods and formicariids in neotropical jungles.) Other similarities between the species of mixed flocks may be convergent adaptations to the same habitat. Each of the species in the flock may have evolved particular characters to be used solely as intra-specific signals; and the fact that the signals of different species are similar may be nothing more than »coincidence» (*i. e.* the physical environment may be such that only certain types of signal can be effective in it). In at least a few cases, however, it does seem probable that the similar signal patterns of several species have become specially adapted to promote the formation and maintain the cohesion of mixed flocks as such.

In some cases, this may amount to real »mimicry» — of a type quite distinct from warning mimicry of either the Mullerian or Batesian types.

A possible or probable example of this phenomenon may be provided by some of the Central American finches of the genera *Volatinia*, *Sporophila*, and *Oryzoborus*.

Several species of these genera are rather similar in plumage color, the males being largely or almost completely black; and many of them tend to associate with one another more or less closely (see, for instance Eisenmann, 1957; Griscom, 1932; Howell, 1957; Skutch, 1954; Sturgis, 1928; and Wetmore, 1943).

Two of these species, the Variable Seedeater *(Sporophila aurita)* and the Blue-black Grassquit *(Volatinia jacarini)* are very common in the isthmian region of Panama. The male Grassquit is almost completely glossy black, with only a small white spot on either side of the body, at the base of the neck, just above the bend of the folded wing. The males of the Variable Seedeater in central Panama are polymorphic; some of them being almost completely black, with only small white spots on either side of the neck, at the base of the primaries, and (usually) on the lower belly, while others have more extensive white areas on the throat and breast as well. The females of both species are largely dull brownish. The two species may be remotely related to one another; but they are quite different in some morphological features, and their display patterns, including voice, are certainly very different indeed. They are both rather gregarious, especially in the non-breeding season. They often feed on the same or similar grass seeds in the same restricted areas at the same time; and frequently occur together in rather loosely organized mixed flocks.

The most common association, in the Canal Zone, consists of one or two Blue-black Grassquits with three or four or more Variable Seedeaters; but the ratio is occasionally reversed. Individuals of the two species may even rest or preen in quite close proximity to one another.

This social grouping of the two species might seem to be entirely casual or »accidental», simply the direct result of their both seeking food in the same places, (especially as they do not display to one another); but there are other indications that the situation is more complicated.

Another species, the Yellow-bellied Seedeater *(S. nigricollis)*, is also gregarious, and also feeds on similar food in many of the same areas at the same time; but it does not associate with either of the other two species as closely or as frequently as they associate with each other — in spite of the fact that almost all its display patterns, including call notes and song, are very similar to or identical with those of the Variable Seedeater.

I have never, however, seen either Blue-black Grassquits or Variable Seedeaters actively avoid Yellow-bellied Seedeaters, or vice versa; and so it is probable that the two former species associate with the latter as often and as closely as would be expected in the case of species which are drawn together by nothing more than similarity of feeding habits.

This would indicate that the special social grouping of the Blue-black Grassquits with Variable Seedeaters is not purely coincidental. There must be some definite positive factors, in addition to feeding habits, which encourage the two species to come together.

These factors are hardly likely to be social behavior patterns alone, as similar displays and flocking habits are not sufficient to bring the Yellow-bellied and Variable Seedeaters particularly close together.

I think, therefore, that plumage color and pattern must be decisive in these cases. The relatively great social isolation of the Yellow-bellied Seedeater must be correlated with the more distinctive color pattern of the male of this species, (the female Yellow-bellied Seedeater is dull brown like the female Variable Seedeater, but the male has a chocolate-colored head, contrasting with lighter brown back, wings, and tail, and dingy white or pale yellow underparts); while the association of the otherwise quite different Blue-black Grassquit and Variable Seedeater must be promoted by the rather similar black plumage of the males, by far the most striking character which the two species have in common. It is probable that both Blue-black Grassquits and Variable Seedeaters are attracted to some extent, or induced to remain longer without retreating or moving on, whenever they see another predominantly black bird of the »correct» size and shape.

I have not yet been able to arrange suitable tests to determine the exact effects of black coloration alone in the social relationships between Variable Seedeaters and Blue-black Grassquits; but the general effect of black can be shown by the reaction of a captive male and female Variable Seedeaters to a group of three male Thick-

Plumage patterns of some Central American finches.

From left to right: 1. adult male Yellow-bellied Seedeater; 2. a dark phase adult male Variable Seedeater; 3. adult male Blue-black Grassquit; 4. adult male Thick-billed Seed-finch.

(The variations in crest shape shown in these sketches are not very significant, as all four species can erect their crest feathers to almost the same maximum extent in certain circumstances.)

billed Seed-finches *(Oryzoborus funereus)* which I introduced into the same aviary. Male Thick-billed Seed-finches are almost all black, with only a little white in the wings. Thick-billed Seed-finches are also supposed to associate with other black or black-and-white finches in various parts of Central America (although I have not yet had an opportunity to observe them in the wild under favorable conditions.) It would seem to be highly significant, therefore, that the captive Variable Seedeaters immediately flew to the Thick-billed Seed-finches (which were not calling or displaying in any way); and then followed the Seedfinches around the aviary for several minutes without any overt indication of hostility. It is also suggestive that some Yellow-bellied Seedeaters in the same aviary ignored the Seed-finches.

The accompanying figure is a diagrammatic sketch of the adult plumage patterns of the male Yellow-bellied Seedeater, a dark phase male Variable Seedeater, the male Blue-black Grassquit and the male Thick-billed Seedfinch.

The resemblance between the Variable Seedeater and the Blue-black Grassquit may be considered a kind of mimicry but it does not seem to be warning. Neither species seems to be particularly »distasteful» to predators. I have fed a small number of both species to a semi-tame Coati *(Nasua narica)* and three captive marmosets *(Oedipomidas spixi)*. The Coati was given three adult male Variable Seedeaters (one in light phase, one in dark phase, and one intermediate), one young male Variable Seedeater (in transition between the dull brown juvenal plumage and adult plumage), one female Variable Seedeater, and one adult male Blue-black Grassquit. The marmosets were given one adult male Variable Seedeater (light phase), two female Variable Seedeaters, one adult male Blue-black Grassquit, and one female Blue-

black Grassquit. All these birds were accepted immediately and eaten with every appearance of relish. (There is also some subsidiary evidence to confirm the palatability of the two species. Neither species shows the »boldness» or confidence so typical of distasteful or poisonous animals. They both usually flee at the slightest alarm.)

The advantages of this rather crude mimicry are presumably purely social. Both species must derive some advantages from their general gregarious tendencies, as shown by the fact that each species tends to form flocks by itself when the other species happens to be absent. (The advantages, in this case, are presumably connected with feeding and/or discovery of predators). It is easy to see, therefore, how they might derive increased advantages from increased gregariousness by joining up with each other.

Mimic relationships of this kind are difficult to distinguish with any degree of certainty; but they may be quite common among birds.

Another possible example among Panamanian birds, for instance, is provided by the White-shouldered Tanager *(Tachyphonus luctuosus)*. The male of this species has a distinctive color pattern, all black with white upper wing-coverts, quite unlike most other tanagers. It is a moderately gregarious species at times, and ranges both inside the forest and along the forest edge. On the forest edge, it usually occurs by itself, singly or in pairs or in small groups; seldom or never joining the mixed flocks of blue, green, and gray tanagers and honeycreepers which are very common in this environment, feeding on both fruits and insects. The only other birds I have ever seen White-shouldered Tanagers join are some of the formicariids which form mixed flocks inside the forest; and it may be significant that the males (at least) of most of these formicariids are also conspicuously marked with black and white. (I might add that I have also seen wintering Black-and-white Warblers, *Mniotilta varia*, associated with such flocks.)

It is even possible that some of the mutual associations of the formicariids themselves (see JOHNSON, *loc. cit.*), and the mixed flocks of chickadees, nuthatches, woodpeckers, etc., in northern woods in Winter, may be facilitated by the black and white markings of many of the species involved.

Such cases would suggest that this sort of social mimicry, when and if it does occur, is roughly comparable to Mullerian Mimicry insofar as the species involved do not have to resemble one another very closely in detail, but only show some of the same conspicuous patterns or colors.

Some of the resemblances between certain calls and notes of distantly related species (MARLER, 1957) may be due to mimicry of a similar type.

The fact that social mimicry may be quite widespread would suggest that some of the cases of supposed warning mimicry in birds should be re-investigated. It is conceivable that social mimicry may play a role in producing certain interspecific relationships which have usually been interpreted as Batesian Mimicry. *e. g.* the associations of a black flycatcher, *Melaenornis pammelaina*, with a black drongo,

Dicrurus adsimilis, (SHEPPARD, 1958), and some of the Moluccan orioles, *Mimeta*, with friar-birds, *Tropidorhynchus*, (WALLACE, 1906).

The advantages which some species may derive from joining each other may also help to explain why certain closely related sympatric species have failed to develop the plumage (and other) differences which might be expected. Such species must be exposed to strong selection pressures in favor of increasing the morphological and/or ethological differences between them, if only to maintain or increase their effective reproductive isolation (see DOBZHANSKY, 1951); but many of them have remained surprisingly similar to one another.

This is true of many gulls and terns, for instance. Many of these birds have retained conspicuous white and light gray coloration, with or without dark patches on head and/or wings. As ARMSTRONG (1946) has already sugested, this light color may serve as a recognition mark, enabling the birds to see and join one another over considerable distances. Different species of gulls and terns will often come together to form mixed flocks on feeding or resting grounds; and this coming together must be facilitated by the similar coloration of so many of the species. Even closer associations are formed by the species which settle together in the same breeding colonies. The Herring Gull *(Larus argentatus)*, the California Gull *(L. californicus)*, and the Ring-billed Gull *(L. delawarensis)* may be cited as examples (see MOYNIHAN, 1956 and 1958). These three species may occur very close together in the same colony, without hybridization, or even any attempts to initiate the formation of mixed pairs. This in quite remarkable, as the three species are very similar to one another in almost all morphological features, differing only slightly in size, proportions, and some flesh colors, and have very similar repertories of social behavior patterns, including homologous hostile, »courtship», and sexual displays, many of which are nearly identical in all three species. (The Herring Gull and the Ring-billed Gull are also connected by the California Gull, which is partly intermediate between them. Some of the characters of the California Gull are almost exactly intermediate between the slightly different characters of the other two species.) The similarities between these three species seem to be greater than those between most other sympatric species, even those, such as some ducks and herons, which have equally long periods of pair-formation and pairing. These gulls seem to be able to maintain their reproductive isolation by recognizing and reacting in an unusually selective fashion to relatively minor differences in morphology and behavior. This would seem to be more »difficult», and may well have taken longer to evolve, than some other methods of maintaining reproductive isolation used by other species. (One would have thought that these gulls could maintain their reproductive isolation more »simply» by evolving a few major differences in plumage pattern — some rearrangement of dark and light areas, for instance — which might be achieved by a relatively small number of mutations.) It is probable, therefore, that these gulls secure appreciable advantages by remaining so similar to one another. The principal advantage may be that their resemblances encourage them to act as if they were all members of a single species

in situations where joint action may be beneficial, (and they certainly do act in this way during defence of the breeding colony as well as during feeding and resting). It is also probable, therefore, that there has been some definite selection pressure in favor of retaining the similarities between the species, a factor which has partly counteracted the selection pressure favoring the accumulation of differences. The existing combination of partial resemblances is probably very much of a compromise.

(2) Neutral coloration

Another type of coloration which is apparently adapted to promote interspecific gregariousness is quite the reverse of the conspicuous and mimetic color patterns listed above. It might be called »neutral» coloration.

It may be illustrated by several more examples drawn from the Panamanian tanagers, especially the Plain-colored Tanager already mentioned above.

The Plain-colored Tanager has most of the special behavior patterns characteristic of highly gregarious species. It is not only very restless, but it also utters call notes very frequently and does a lot of wing- and tail-flicking. All this is quite conventional; but its plumage pattern is rather more peculiar in some ways. Both males and females are dull gray, with blackish wings and tail (and small patches of bright blue on the upper wing-coverts, which are seldom revealed except in flight). These wing and tail colors are flash patterns of the usual type; but the dull gray of the rest of the plumage is really the most remarkable feature of the species. Such dull coloration is very rare among tanagers, most of which are very brightly colored, with large areas of red, yellow, green, blue, and/or white, often combined in intricate patterns. It seems probable, therefore, that the drab color of the Plain-colored Tanager subserves a special function. This can hardly be concealment, as the gray is far from cryptic under natural conditions. Plain-colored Tanagers moving through the foliage in which they feed are far more easily seen than birds with green plumage (such as some of the female honeycreepers which also occur in the same places). The real function of the dull gray color would seem to be social. Plain-colored Tanagers are not only highly gregarious among themselves, often forming flocks of their own species alone, but they are also frequently associated with other species in mixed flocks of considerable size. Many species of tanagers, honeycreepers, and other birds, which forage along the forest edges or inside light second-growth forest will join one another in mixed flocks during feeding periods; and the great majority of such flocks around Barro Colorado are composed of a group of Plain-colored Tanagers plus smaller groups, pairs, or single individuals of many other species. (Some of these flocks may include at least eight species at the same time.) The Plain-colored Tanagers are usually the »nucleus» of such flocks. They seem to attract many of the other species, »set the pace» for many of the group activities, and determine the direction of the major movements of the flock. The males, and sometimes both sexes, of almost all the species associated with the Plain-colored Tanagers in such flocks (with the excep-

tion of the Palm and Blue Tanagers, both of which are discussed below) are very brightly and/or conspicuously colored. Most of them are largely bright blue and/or bright green, sometimes conspicuously marked with black, in patterns which are very different in different species. Among these species are the Blue and Shining Honeycreepers *(Cyanerpes cyaneus* and *C. lucidus)*, the Green Honeycreeper *(Chlorophanes spiza)*, the Ultramarine and Scarlet-thighed Dacnises *(Dacnis cayana* and *D. venusta)*, the Golden-masked Tanager *(Tangara larvata)*, and the Blue Cotinga *(Cotinga natterii)*. The dull coloration of the Plain-colored Tanager would seem to be a specific adaptation to help the species play its role in such mixed flocks. It seems to be effective just because of its very dullness, its neutral quality. If the Plain-colored Tanager were more conspicuously colored, it might be less attractive to, or exert less influence upon, its associates of other species. In general, the more distinctly different two birds are in appearance, the less likely they will be to join one another. The drab appearance of the Plain-colored Tanager probably makes it look less different to its brightly colored associates than it would if it had a distinctive bright pattern of its own. Of course, the Plain-colored Tanager might be even more effective in attracting other species if it could develop the same conspicuous colors and patterns as theirs; but most of the species with which it associates are so different from one another that it would be very difficult or impossible to mimic them all. The Plain-colored Tanager seems to have evolved a »compromise» type of coloration instead, one that is moderately different from those of almost all its associates, without being too conspicuously different from any. The fact that the compromise, neutral, coloration is drab may also have another advantage. It may make the other signal patterns of the species, the restlessness, calling, flash patterns of wings and tail, and flicking movements, relatively more effective than they would be otherwise. The drabness may allow the other characters to attract and hold a greater share of the attention of observers.

One might expect that the other species which join the flocks of Plain-colored Tanagers would have evolved in the same direction (as they presumably also derive advantages from the association); but most of them have not done so. This is probably due to the fact that most of them are purely casual associates. The Plain-colored Tanager is a regular member of the mixed flocks; but the composition of the rest of the flocks may vary considerably at different times. Most of the other species only join occasionally.

The two exceptions to this general rule are the Palm and Blue Tanagers *(Thraupis palmarum* and *T. episcopus)*. Both species are quite gregarious, the Palm Tanager more than the Blue Tanager, although less so than the Plain-colored Tanager. Both species are also fairly regular members of the same mixed flocks as the Plain-colored Tanager. There are usually more Palm Tanagers than Blue Tanagers in such flocks, although both are usually outnumbered by Plain-colored Tanagers. It would seem to be highly significant, therefore, that both the Palm and Blue Tanagers are more drably colored than many other tanagers, and that the Palm Tanager is duller than

the Blue. The Palm Tanager is dull olive green, with blackish wings and tail; and the Blue Tanager is dull grayish blue, somewhat brighter on the wings and tail. The fact that both species have much the same type of coloration as the Plain-colored Tanager is probably due to convergence and is not an indication of close relationship. (Both the Palm and Blue Tanagers are rather different from the Plain-colored Tanager in some morphological details, and quite different in display patterns, including call notes and song.) This convergence of plumage patterns would seem to support or confirm the interpretation of the Plain-colored Tanager's plumage suggested above.

(It should also be mentioned that the Golden-masked Tanager, which is undoubtedly closely related to the Plain-colored Tanager and has very similar displays, but is only a casual or occasional member of the mixed flocks, has a very brightly colored and elaborate plumage pattern, quite different from that of the Plain-colored Tanager.)

(3) General comment

These cases of special social relationships between different species have been described at some length in order to emphasize the general importance of such relationships. It will usually be advantageous for any reaction between any two species to be as definite as possible, either positive or negative — if only because a definite response of any kind will usually be more rapid than any kind of inconclusive or ambivalent reaction. This means that there will usually be strong selection pressures either for or against the development of particular resemblances or lack of resemblances between any two species which ever come into contact with one another.

ADAPTATIONS TO CONTROL HOSTILITY

The adaptations designed to promote gregariousness indirectly, by controlling potential hostile responses, are usually less obvious than the characters adapted to increase gregariousness directly. They have certainly been less studied.

Both morphological and ethological characters may help to control hostility; but it will not be necessary to discuss the morphological characters separately, as they are all strictly correlated with particular behavior patterns, and do not include such distinctive categories of releasers as conspicuous coloration or flash patterns.

Most of the ethological adaptations designed to control hostility can be divided into a few major types.

The one thing which even the most highly gregarious species have apparently been unable to achieve is the complete suppression of hostility. It might be expected, nevertheless, that they would show less potential hostility than less gregarious species in similar circumstances; but even this may be only partly true in some cases.

There are only a few species which may have been able to reduce hostility directly, in the course of evolution, by reducing the potential strength of the internal attack and escape drives (or the »specific action potentials» or »reaction specific energy» of the attack and escape tendencies). Some highly gregarious species do seem to show

hostility in all or almost all the same circumstances as less gregarious species; but tend to show this hostility, both ritualized and unritualized, in rather weaker forms. The Plain-colored and Palm Tanagers may illustrate this phenomenon also. They both tend to show a lot of hostile behavior patterns in their flocks; but most of these patterns, including a variety of pure attack and escape movements, ambivalent combinations and alternations of advance and retreat intention movements, hostile notes, and a few threat postures and movements, are brief, simple, and apparently low intensity. The Plain-colored and Palm Tanagers seem to show fewer elaborate and apparently high intensity hostile displays than most of the less gregarious tanagers, *e. g.* the Crimson-backed Tanager or Sangre de Toro *(Ramphocelus dimidiatus)*, living in the same environment. This might be due to some general reduction in strength of hostile motivation; but the same effect might also be produced by habituation, as all the members of a semipermanent or long-enduring flock might be expected to become habituated to one another. It is unfortunate, therefore, that none of the species which exhibit this widespread reduction of overt hostility have been studied in sufficient detail to determine the precise cause(s) of their apparently weak attack and escape behavior.

I should mention, in passing, that although habituation to other members of the group must be adaptive in many cases, it is probably not a special adaptation to increased gregariousness. There seems to be no evidence to indicate that habituation is faster or more frequent in highly gregarious species than in less gregarious species in the same social situations. In fact, if it is advantageous for some moderate degree of hostility to be maintained within a flock — as it probably is in many cases, since so many highly gregarious species do show an appreciable amount of intra-specific hostility — then it is quite possible that many highly gregarious species will eventually be found to be less easily habituated than most less gregarious species.

Although some birds may have achieved a general reduction of their internal attack and escape drives, it is obvious, I think, that most gregarious birds have evolved other means of controlling potential hostility.

Many of them seem to have become less responsive to certain particular sign stimuli, without having reduced their reactions to other stimuli. Their hostility seems to have become confined to a comparatively restricted number of situations; but tends to be as strong as that of more solitary species when it does occur. This sort of restriction may be illustrated by the peculiarly limited territorial hostility of many colonial-nesting species, such as gulls, terns, and icterids, which may show intense hostility toward other animals and objects within a particular small area, and no hostility at all to the same animals or objects outside the area. Some of the well-known dominance hierarchies which some social species may develop in their flocks (especially in the confined spaces of captivity) may be roughly analogous, insofar as any member of the hierarchy may show great hostility toward certain other members, while largely ignoring the remainder.

Another common, perhaps the most common, type of adaptation designed to control hostility in gregarious birds is the development of special behavior patterns

to »dissipate» hostility in relatively harmless ways. Some moderately and highly gregarious species may show as much high intensity hostility, in much the same range of situations, as less gregarious forms, but have evolved special methods of apparently unritualized fighting or ritualized displays through which this hostility can be expressed without too much damage to the social group or flock.

A moderately gregarious species which seems to have developed a rather harmless method of unritualized disputing is the Green Honeycreeper. Whenever two Green Honeycreepers (except the male and female of a well-established pair) come within a few yards of one another, they almost always start to show intense hostility at once. Some of their hostility takes the form of display (see below); but the remainder usually consists of a long series of remarkably vigorous attack and escape movements which are so »arranged» that the birds seldom or never come into actual physical contact with one another. One bird will make an obviously unritualized flying rush, a »supplanting attack» on the other; while the latter simply escapes immediately. The aggressor follows, until its opponent stops escaping (usually a few yards away), whereupon the aggressor also stops, just short of its opponent. The chase may be resumed after a short pause for rest or display, and the original aggressor may make supplanting attack after supplanting attack, stopping just short of its opponent each time, after the latter has fled a short distance away each time. Or the two birds may reverse and alternate roles, first one attacking and then the other, in a specta-

cular see-saw back-and-forth »battle» in which no blows are struck. These disputes may continue for minutes on end, even in the feeding areas where the birds do not hold territories in the conventional sense. (This form of hostility is only successful in the wild. In captivity, the restrictions break down, and one bird usually manages to kill the other within a very short time.) Roughly similar chasing and escaping is, of course, very common during the hostile encounters of many other birds; but the Green Honeycreeper's successive supplanting attacks and see-saw disputes seem to be more frequent and more regular than those of most other species (certainly more regular than those of other honeycreepers and tanagers in the same environment on Barro Colorado Island).

Other species of birds have developed several different kinds of special display behavior.

Many highly gregarious species seem to express more of their hostility through display than less gregarious species; but use displays of the same ordinary, »conventional», type, *i. e.* ordinary threat and appeasement, as the more solitary species. In other words, the more solitary species may show threat and appeasement displays only when the attack and escape drives are nearly equal in strength, and perform overt unritualized attack and escape movements whenever one of the hostile drives is moderately stronger than the other; while the more gregarious species may perform threat and appeasement displays in both situations, only performing overt attack and escape movements when one of the hostile drives is really overwhelmingly stronger than the other. This may be illustrated by the contrast between the White

Noddy or Fairy Tern *(Anoüs albus)* and other gulls and terns. The White Noddy is less gregarious than most other gulls and terns, and it performs fewer threat and appeasement displays and more unritualized attack and escape movements than its more highly social relatives, even the rather closely related Brown and Black Noddies *(A. stolidus* and *A. minutus)* which live in the same environment (personal observation).

On general theoretical grounds, one might expect that highly gregarious species might have more different types of appeasement displays, and use them more frequently, than less gregarious species; but there is little or no evidence to support this at the present time. It is possible that most appeasement displays are used during encounters between mates and potential mates, and are relatively unimportant during non-reproductive social encounters.

Other highly gregarious birds have evolved hostile displays of a less conventional type than either threat or appeasement. Among these are the so-called »deceptive» displays and the very contagious »mimetic» or »exemplary» displays, shown by such species as the Spice Finch *(Lonchura punctulata)*, the Jackdaw *(Corvus monedula)*, the Swallow-Tanager *(Tersina viridis)*, and the Oystercatcher *(Haematopus ostralegus)*, which dissipate or divert hostility in a variety of different ways, by stimulating communal performances which prevent fighting between particular members of a group, or by releasing particular non-hostile behavior patterns, (see MOYNIHAN and HALL, *op. cit.*, LORENZ, 1952, SCHAEFER, 1953, and MAKKINK, 1942, as well as the discussion in MOYNIHAN, 1955).

The possibly very great importance of adaptations to control hostility may be illustrated by a final example from among Panamanian birds, the three common and closely related honeycreepers which have already been cited above in several connections, the Blue, Green, and Shining Honeycreepers.

These three species seem to have similar positive gregarious tendencies; but they usually occur in social units of very different size under natural conditions.

Around Barro Colorado, the Blue Honeycreepers often occur in moderately large and stable flocks of approximately six to twelve birds (at least in the non-breeding season), and the Green Honeycreepers occasionally form large but unstable flocks for comparatively brief periods, while the Shining Honeycreepers seldom or never occur except singly or in pairs (of their own species — they do sometimes join mixed flocks of other species).

A crude indication of the direct, positive, gregarious tendencies of such birds can be obtained by placing captive individuals outside in a cage in their natural environment; and then seeing how frequently they are visited by wild birds which do not attempt to attack or threaten them without provocation. I have done this with all three species of honeycreepers, in a series of tests extending over a period of six months; and the results of these tests would indicate that captive individuals of each species are about equally likely, on the average, to receive »friendly» visits from wild individuals of their own species. In other words, a captive Shining Honeycreeper is just about as likely to be visited by wild Shining Honeycreepers as a captive Blue

Honeycreeper by wild Blue Honeycreepers. (This is only a very rough estimate, as the total populations of the three species around Barro Colorado are obviously rather different — although they are all fairly common in the particular areas where the tests took place.) These tests would suggest that the great differences between the three species in actual gregariousness under natural conditions must be due to something other than differences in the strength of their tendencies to approach and join one another.

I think that most of these differences in actual gregariousness may be explained by differences in hostility.

Individuals of all three species are rather aggressive toward other members of the same species; but they usually express their aggressiveness in very different ways.

Blue Honeycreepers express most of their aggressive hostility by display, especially calls which seem to be both threat and exemplary (*i. e.* mildly intimidating and very contagious at the same time). They show relatively very little overt attack and escape during most intra-specific disputes. Thus any group of Blue Honeycreepers, no matter how or why it has been formed, is unlikely to be violently disrupted by hostility; and the factors promoting social solidarity will be allowed to operate with relatively little disturbance. Green Honeycreepers express most of their aggressive hostility by rigid threat postures and movements, and the peculiar fighting described above, which may tend to disrupt a flock, but not necessarily completely or absolutely immediately. Shining Honeycreepers express most of their hostility by threat calls which are usually accompanied by violent overt attack, culminating in furious pecks at the object of the attack. Thus, whenever two Shining Honeycreepers (except mates) come together, one of them will usually be forced to flee at once in order to escape serious injury or death; and there will be little or no chance for any factors promoting sociability, apparently present in this species as well as the others, to come into operation.

It is evident, therefore, that the general social evolution of this group of honeycreeper species has involved changing their hostile responses rather than their tendencies to come together as such. (And this must be true no matter what direction their social evolution has followed, whether they have become more gregarious than their common ancestor, or less.)

COMMENT

This brief list of some adaptations promoting gregariousness may have shown how diverse they are, and how little is known about most of them. It is obvious, of course, that the same objectives can be attained by very different types of adaptations, and that similar types of adaptations can subserve very different functions; but the precise ways in which particular characters, especially behavior patterns, can affect the social relationships between birds of the same or different species have not been studied as thoroughly as they should be. Most of the more intensive studies of bird behavior in the field have been more interested in analyzing the existing social

relationships within a given group than in attempting to discover how the group was originally formed or how it is maintained in the face of the disruptive influences which are always present in the physical and social environments. Most studies have also been primarily concerned with analyzing the immediate causation of social behavior patterns; but it is just as necessary to determine the exact functions of such patterns in order to understand their evolution, and therefore their ultimate causation.

Summary

A bird usually reacts to the presence of other birds by showing several contradictory tendencies. It is usually partly »friendly» and partly hostile, apparently wanting to join the other birds peacefully, and yet also wanting to attack and/or escape from them at the same time. The resolution of such conflicting tendencies is particularly complex in the more highly gregarious species, which have had to evolve special characters to promote the general social or flocking tendencies, and/or other characters to control the hostile responses which are almost inevitably provoked by any close association of different individuals.

Among the characters which seem to be adapted to promote gregariousness directly, by increasing or facilitating the tendency of birds to join one another, are conspicuous coloration, flash patterns on wings, rump, and/or tail, call notes, ritualized flying intention movements, and increased general mobility or restlessness.

Some special characters seem to be primarily or exclusively designed to promote the formation of mixed flocks of several species. Among these are »neutral» coloration and a type of (non-warning) social mimicry.

The adaptations which help to control potential hostility include general reduction of the internal attack and escape drives, partial loss of responsiveness to certain particular hostile stimuli, and the development of special fighting and/or display behavior to dissipate hostility in relatively harmless ways.

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Factors Affecting Reproduction of the Canada Goose (*Branta canadensis*)

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This paper deals with the inter-relationships and relative effects of some of the factors influencing the early stages of the reproductive period in certain populations of Canada Geese *(Branta canadensis)*. An attempt has been made to evaluate the significance of varying reproductive success with respect to population stability.

Exploratory field work was commenced in 1948. In 1949 extensive observations were made in the marshes of the upper Columbia Valley, British Columbia, and the breeding area on Goose Island in the same region was inspected for the first time. By 1950 it had become apparent that intensive study of geese breeding on islands would be most likely to yield information on the operation of density-dependent factors influencing reproductive success. This seemed a most promising line of investigation and so in that year the breeding area on Hatfield's Island in the southern Okanagan Valley, British Columbia, was studied and from then until 1953 attention was focused on the two island populations.

Nesting areas were visited in early April at the time when nest sites were being selected and egg laying was commencing. In late April the nesting areas were carefully searched for nests. During the study, data on 405 nests were obtained at the time of their commencement. In late May the nesting areas were visited again to determine the fate of eggs in previously marked nests. Complete histories of 378 nests containing 1,907 eggs were determined.

The areas where the study was carried on are both mountain valleys in the Cordilleran region of western Canada. Goose Island is situated near the center of a 150-acre marshy lake on the east side of the Columbia Valley. It is about 1.5 acres in area. There is a gravel beach about 2 to 5 yards in width around the island and steep banks 60 feet high at one end and 25 feet at the other rise from the beach. In scattered formation a few Douglas fir *(Pseudotsuga taxifolia)*, and thickets of juniper *(Juniperus communis)*, mountain birch *(Betula fontinalis)*, rose *(Rosa nutkana)*, and

willows (*Salix* spp.), cover half of the island top, the remainder supporting a rather sparse growth of range grasses and sage brush (*Artemisia* spp.).

Hatfield's Island, the principal nesting site for Canada geese in the Okanagan Valley, is situated near the south end of Vaseaux Lake. The area of the island is 3.6 acres. On the higher areas mature ponderosa pine *(Pinus ponderosa)* grow. An undergrowth of mountain birch, red osier dogwood *(Cornus Nuttalli)*, wild rose, willows and black hawthorn *(Cratægus Douglasii)*, forms a narrow tangle all along the shore down to high-water line. There are no beaches.

It was initially attempted to obtain the following data:

(1) Sizes of the breeding populations

(2) Numbers of nests commenced

(3) Numbers of eggs contained in the nests

(4) Precise fate of all eggs laid

(5) Fate of goslings during their first eight weeks of life (*i. e.* until attainment of flight).

In addition, as an aid in interpreting the quantitative data observations of behaviour were made from time to time during the periods of establishing nesting sites, laying, incubation and brooding.

TERRITORIAL BEHAVIOUR

Observed behaviour indicates that there is an inverse relationship between territorial competition and the success in hatching young of the individual pairs making up the population. In other words, the breeding success of any pair is likely to be reduced by the intense territorial competition which occurs when the population is over-crowded. Data relating to hatching success of different time-place groups of clutches, which will be presented later, also support the contention that territorial antagonism limits success in hatching young of some individual pairs.

In observing geese during the period of nest establishment it was noted that on some occasions pairs came near each other with no evidence of antagonism. More frequently definite disturbances resulted from their close contact. For example, between 8.30 and 9.45 a.m., on April 15, 1952 a pair of geese made six attempts to land on Goose Island and was each time rebuffed by geese apparently already in possession of territories. It was noted generally that the geese which had not established nests exhibited antagonistic behaviour from time to time but those which were already incubating or laying eggs did not so often become involved.

Besides the observed behaviour there is indirect evidence to support the contention that some females that are ready to lay eggs are unable to occupy sites and build nests in which to lay. Reference is made to numbers of randomly scattered, undamaged eggs found at various points on Goose Island but most commonly on the top. It seems likely that some birds, probably having arrived on the breeding area slightly later than most, were unsuccessful in gaining or maintaining possession of a nesting site and were thereby forced to drop eggs on the ground.

CLUTCH SIZE

Other nesting studies of Canada Geese (Williams and Marshall, 1937; Dow, 1943; Jensen and Nelson, 1948) indicate that the average number of eggs in Canada Goose clutches is very close to five. The mean size of all clutches examined in 1950 through 1953 on Goose Island was 5.44, and of all clutches examined in the same years on Hatfield's Island, 4.92. In each individual year mean clutch size on Goose Island exceeded that on Hatfield's Island. In general the range of clutch size was greater on Goose Island than on Hatfield's Island (Fig. 1). Because of the variability within the data from each area the difference between the mean clutch sizes cannot be established as statistically significant. However, a chi square test of the relative occurrence in the two areas of large clutches, (*i. e.* those containing seven or more eggs) reveals a highly significant departure from expected occurrence (p. = .001). It may be concluded, therefore, that the tendency for Canada Geese breeding on Hatfield's Island to produce fewer large clutches than those breeding on Goose Island is significant.

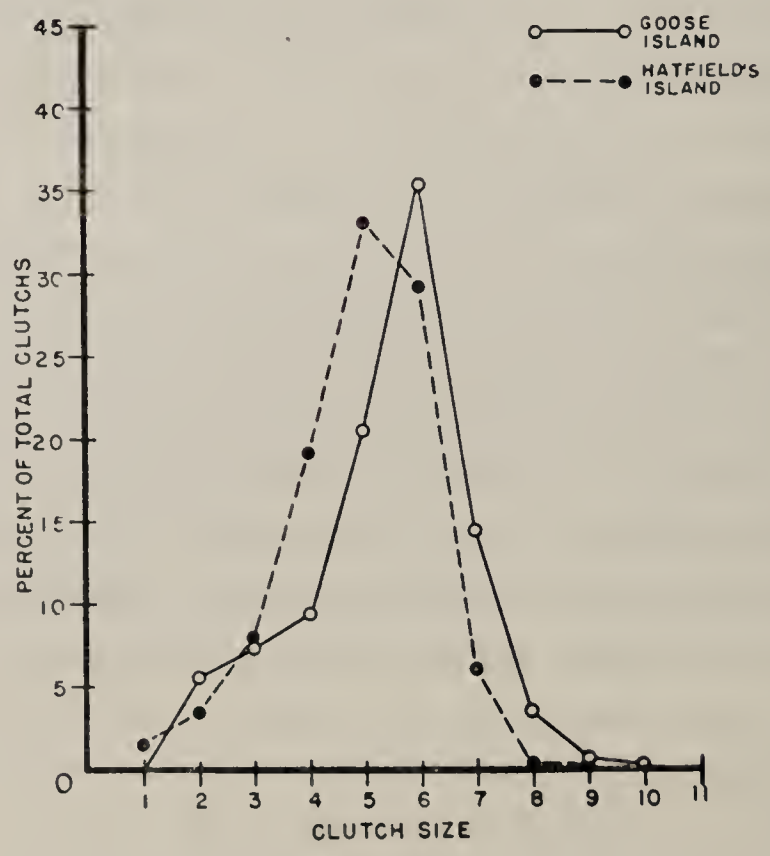

Fig. 1.

Investigation of the factors influencing egg production has been largely confined to domestic birds. Workers have found that production of chicken eggs may be affected by environmental factors such as a variation in the period of exposure to light and availability of essential nutrients, and by genetic factors, the operation of which may, of course, be influenced by in-breeding and out-breeding. The distribution of age classes within populations may also affect the rate of egg production in domestic birds, the younger birds tending to produce fewer large clutches. The differences in egg production between groups of Canada Geese described above might be caused by differences in age-class composition of the populations or by environmental

or genetic factors. However, it seems unlikely that an unusual preponderance of older birds could long exist in a wild goose population and in the case in point a genetic cause is thought to be more likely. Two factors must be considered, namely, the prevalence of large clutches on Goose Island, and the greater range of clutch size there. Geese breeding on Goose Island are a small group in the midst of the much larger upper Columbia Valley population and are thus in a position advantageous for gene exchange with a large number of birds. The Hatfield's Island birds, on the other hand, are relatively isolated from other geese, at least on the breeding ground, and this isolation may be maintained throughout the year by behavioural mechanism. It would be expected that frequent gene exchange would favour greater egg production, a manifestation of hybrid vigour, and greater range in clutch size. Conversely it may be expected that limited gene exchange would result in reduced egg production. While the effect of favourable environmental factors might also be to increase production, it would be unlikely that the same factors would cause a greater range of clutch sizes. There remains the possibility that at some point in their range, not necessarily on the breeding grounds, the Hatfield's Island geese are influenced by environmental factors unfavourable to maximum egg production. It might be suspected, though, that were such the case there would be other manifestations of ill health or debility among the Hatfield's Island geese. There is no such evidence. Therefore, it is thought that a genetic factor is the most likely cause of the observed differences in egg production.

NESTING DENSITY

The term »nesting density» refers to the relation between the total number of nests in an area and the size of the area. Such data indicate for the area to which they refer how many members of the total potential breeding population successfully commenced laying. Nesting density is not necessarily a measurement of the total potential breeding population because, as has been pointed out previously, when a population is at a high level territorial antagonism operating in a crowded area apparently prevents some birds from progressing through the breeding cycle to the point of laying in nests.

Canada Geese generally do not exhibit a high nesting density, but on small islands high densities may be found. On Goose Island and Hatfield's Island, nesting densities varied from 9.4 to 30.7 nests per acre. Effective densities were even higher than the data indicate. For example, in 1950 on Goose Island 34 of 45 nests in which laying commenced were located on the beach or steep banks of the island, which constituted not more than one-half of the total area of about 1.5 acres. The mean of all distances measured from each nest to its closest neighbour was 22 feet. On Hatfield's Island there was a grouping of nests into three concentrations, which similarly increased the effective density over that which can be accurately calculated. There in 1950 the mean distance between each nest and its closest neighbour was 28 feet.

HATCHING SUCCESS

Data on hatching success of nests in the upper Columbia Valley marsh and on Goose Island and Hatfield's Island are given in Table 1.

TABLE 1

Mean Clutch, Mean Hatch and Mean Per Cent Hatch

(Bracketed figures are numbers of variables from which means are derived.)

	1949	1950	1951	1952	1953
Columbia Valley Marsh					
Mean complete clutch ...	5.50 (36)	4.73 (11)	5.28 (7)	—	—
Mean hatch.....	3.68 (38)	4.11 (9)	—	—	—
Mean % hatch	67.8	85.7	—	—	—
»*Goose Island*»					
Mean complete clutch ...	5.09 (11)	5.38 (42)	5.56 (46)	5.24 (21)	5.47 (34)
Mean hatch.....	4.00 (9)	3.90 (42)	4.42 (45)	3.88 (18)	4.80 (35)
Mean % hatch	76.5	71.6	76.7	69.5	88.6
Hatfield's Island					
Mean complete clutch ...	—	5.17 (36)	5.10 (51)	4.83 (49)	4.72 (61)
Mean hatch.....	—	4.53 (34)	4.97 (33)	3.54 (48)	3.31 (63)
Mean % hatch	—	87.6	96.4	70.5	63.4

Several of the terms used in Table 1 require some explanation. Mean hatch is the total number of eggs known to have hatched divided by the total number of nests of known history. It represents the mean productivity to the hatching stage per breeding pair. Mean hatch for all clutches studied was 4.00. Mean percent hatch is the average of the percent of eggs hatching from each clutch. It relates hatching to commencement of nests irrespective of size of clutches. The percentage relation of eggs hatched to those laid indicates the relative productivity of populations but differs from mean percent hatch in that it does not show as strikingly the effect of such factors as desertion, which reduce success by affecting entire clutches. Thus on Hatfield's Island in 1950 when desertion was an insignificant cause of loss, mean percent hatch was 87.6 and percentage of eggs hatched was 87.5. In 1953, on the other hand, when desertion was the outstanding loss factor, mean percent hatch was 63.4 and percentage of eggs hatched was 71.7.

Data on fate of eggs are summarized by areas in Table 2.

The causes of failure to hatch are discussed now in the order of their importance.

DESERTION

Desertion of the clutch by the incubating female was noted during the study to be the most important cause of failure of eggs to hatch, accounting for 41.7 percent of all failures. Of eggs of known history 8.4 percent were deserted. In some instances

TABLE 2

Fate of Eggs by Areas

	»Goose Island« (%)	Hatfield's Island (%)	Columbia Valley Marsh (%)	Total (%)
Total eggs laid	793 (100.0)	859 (100.0)	255 (100.0)	1907 (100.0)
Hatched	637 (80.3)	696 (81.0)	190 (74.5)	1523 (79.9)
Deserted	61 (7.7)	97 (11.3)	2 (0.8)	160 (8.4)
Predated	23 (3.0)	33 (3.9)	4 (1.6)	60 (3.2)
Displaced from nest	26 (3.3)	3 (0.3)	5 (1.9)	34 (1.8)
Infertile	9 (1.1)	15 (1.7)	11 (4.3)	35 (1.8)
Death late embryo.....	3 (0.4)	5 (0.6)	17 (6.7)	25 (1.3)
Flooded	—	—	23 (9.0)	23 (1.2)
Death early embryo	8 (1.0)	5 (0.6)	3 (1.2)	16 (0.8)
Adult killed.....	12 (1.5)	—	—	12 (0.6)
Unknown.....	14 (1.8)	5 (0.6)	—	19 (1.0)

the relationship between desertion and predation may complicate interpretation of nest histories since crows *(Corvus brachyrhynchos)* or magpies *(Pica pica)* may eat deserted eggs, or geese may desert their nests after some of the eggs have been destroyed by predators. In 16 cases there were losses of parts of clutches due to predation. In eight of these, geese continued to incubate and the remaining eggs subsequently hatched. This is considered to be clear evidence that predation of part of the clutch is by no means always followed by desertion of the remainder. In the eight other cases involving predation, the remaining undestroyed eggs were deserted. The question arises whether desertion or predation came first and which should therefore be considered the primary cause of loss. Since the evidence in cases involving both predation and desertion cannot be used to determine which was the primary cause, the losses have been categorized in accordance with their apparent, although possibly secondary, causes. It is suspected that this interpretation may minimize the importance of desertion.

It is considered unlikely that the activities of the observer had any significant effect on the rate of desertion, because were such the case one would expect that nests well removed from the nearest neighbour but visited just as frequently by the observer would be equally likely to be deserted. That was not so.

Desertion was found to be closely related to the distance between nests. Mean distance between nests may be considered a measure of crowding or density. It will be recalled that in 1950 on Goose Island the mean distance between each nest and its nearest neighbour was 22 feet. A mean distance similarly calculated but involving successful nests only was 25 feet, while the mean distance between nine deserted nests and their closest neighbour was only 10 feet. It was found that when nests were built less than 10 feet apart, one of the two so located would be deserted, and that there was some likelihood of desertion when nests were within 15 feet of each other. Thus, of eight nests which were 10 feet or less from their neighbour, five were deserted

and of 11 which were between 10 and 15 feet apart, two were deserted. Of the two other nests on Goose Island which were deserted in 1950, one was 18 feet from its closest neighbour, the other 35 feet.

TABLE 3

Egg Losses Due to Density-Dependent Factors

Desertion and displacement of eggs from nest

	Hatfield's Island				»Goose Island»			
	1950	1951	1952	1953	1950	1951	1952	1953
Density Nests/acre.....	9.4	14.2	14.2	16.7	29.3	30.7	18.7	23.3
Per cent loss due to density-dependent factors	1.2	3.0	17.0	18.9	18.9	12.3	14.7	0.6

Nest densities, that is to say numbers of nests per acre, are also a measure of crowding. In Table 3, nest densities on Goose and Hatfield's Islands are compared with per cent losses of eggs due to desertion and displacement of eggs from the nest. Because both causes are thought to be largely density-dependent they are considered together here, and the phrase »desertion and displacement» will be employed to refer to the two causes.

On Hatfield's Island there is apparent a progressive increase in the loss of eggs through desertion and displacement from 1950 to 1953 coincident with an increasing density. Comparison of the data from Goose Island for 1950 and 1951 with those from Hatfield's Island for the same years suggests a close correlation between desertion and displacement, and density. The data which do not seem to fit the proposition are those from Goose Island for 1952 and 1953, and to a lesser extent those from Hatfield's Island for 1951 and 1952, when the density remained constant and the loss due to desertion increased strikingly. How are these apparent discrepancies to be interpreted?

There is a fundamental difference between the populations of the two islands which could have a very significant effect on variations in the actual breeding populations. The Goose Island group is but a small part of the aggregation of geese which breed throughout the flood plain of the upper Columbia Valley. The Hatfield's Island group, on the other hand, is the major component of the Vaseaux Lake population of geese. It might be expected then that the Goose Island group would be affected by changes in size and local distribution of the Columbia Valley population and by territorial behaviour of geese in the adjacent marshes, while the Hatfield's Island group would be practically independent of the influence of other populations. Interpretation of the Goose Island data may thus be complicated by unmeasurable population shifts between the Goose Island group and the surrounding population, and proof of the existence of very real population factors may thereby be obscured.

Evidence has been presented to show that on Goose Island at least the effect of territorial antagonism was such that potential breeding birds could have been prevented from laying eggs in nests. It will also be recalled that a number of randomly dropped eggs were found there. It seems reasonable to assume therefore that the potential breeding population may often exceed the actual breeding population. There is no direct evidence to indicate that in 1952 the potential breeding population on Goose Island was as great as, or greater than, in 1951, but neither is there any contrary evidence. General observations on numbers of geese present did not suggest the total number of birds present had decreased, even though the number of nests found was smaller. Observations made in April, 1952 indicated that there was a high degree of competition for nesting sites on the island, such as might be commensurate with a crowded population. It seems possible then that a number of mature geese, even greater than that present in 1950 and 1951, by their intense competition for nesting sites reduced the number of birds successful in commencing nests to a point below that which had been attained in previous years. Since antagonism between nesting birds and those unsuccessful in establishing nests would continue for at least a short period after incubation commenced, the density effect would also continue to operate on nesting birds and result in a loss due to desertion and removal of eggs from the nest of the same order as that noted in previous years, even though the actual nesting population had declined.

How may we explain the remarkable situation at Goose Island in 1953, when loss due to the density-dependent factors was less than one percent, yet the number of nests per acre was 23.3, the third highest recorded there? If the other evidence which has been presented is sufficient to demonstrate that desertion and removal of eggs from the nest are indeed density-dependent one must suspect that on Goose Island in 1953 the potential nesting population was at a level nearly optimum for hatching success. One can speculate that the potential nesting population of the Columbia Valley as a whole was lower than in the previous years or that the pressure which it exerted on the Goose Island group was somehow reduced. Population estimates for the Columbia Valley as a whole based on aerial surveys suggest that the former possibility is unlikely. However, there may be variations in the goose distribution pattern within the valley, perhaps related to water levels or to fluctuations in muskrat populations and consequent availability of muskrat lodges for nesting sites, which might sometimes cause the pressure of the whole population on the Goose Island group to be disproportionate to its size.

On Hatfield's Island there was a fairly consistent increase in nesting density and in loss of eggs due to desertion between 1950 and 1953, although in 1951 and 1952 densities were the same while losses due to desertion increased notably. A possible explanation of this discrepancy is that the potential nesting population may have increased in 1952, as was suggested to have been the case at Goose Island in the same year. If such were the case one might wonder why the number of nests actually commenced was not reduced as it was at Goose Island in 1952. A habitat difference may

be the key to this question. Goose Island has open gravelly beaches which in spring, when the geese arrive and before the water level begins to rise, may be as much as 20 feet in width. Furthermore, the line of trees and shrubs which borders the upper edge of the beach, while dense in places, is by no means impenetrable. The top of Goose Island is largely open, there being but a few Douglas fir and juniper scattered upon it. Hatfield's Island, on the other hand, has no beaches, and an extremely dense riparian shrub complex closely adjoins and largely overhangs the water's edge. Geese seeking nesting sites on Hatfield's Island can do so with much less risk of detection and interference by other geese than can the Goose Island birds, which must advance toward the nesting areas across an open strand. Geese on Hatfield's Island thus may be able to establish nests more readily. BALHAM (1954) has stated that the size of the territory defended by geese attains a maximum at the time incubation commences and then steadily decreases. Territorial antagonism thus usually does not become fully effective during the period of nest establishment and egg laying, and on Hatfield's Island its effect may be additionally inhibited because good cover reduces the likelihood of contact between potentially antagonistic pairs. In other words, on Hatfield's Island, due to superior cover, there may be a vital time-lag in the consequences of high population density.

EGGS DISPLACED FROM THE NEST

The loss of eggs through their becoming removed from the nest accounted for 11.5 percent of all hatching failures. This type of loss is related to the physical characteristics of the nesting site as well as nesting density. Eggs may become dislodged from the nest while the female is turning them, or, if she is suddenly flushed from the nest as the result of a disturbance caused by neighbouring geese or some other agent, she may kick them out. This sort of loss was frequent on Goose Island, where the majority of the nests are located on or near fairly steep banks. Considering the intraspecific antagonism that is a feature of the behaviour of the geese on Goose Island at the beginning of the breeding season, it seems likely that the eggs were knocked out of the nest while geese were engaged in territorial dispute.

PREDATION

Predation was the second most important cause of egg loss, accounting for 15.6 percent of the total egg loss, and 3.2 percent of all eggs laid. All remains of predated eggs found on Goose Island and Hatfield's Island exhibited the characteristics of corvid predation. Predation was of irregularly varying importance from year to year.

In 1953 predation of incubating females was noted for the first time on Goose Island. On May 22 two dead Canada geese were found, each near a nest. A pair of bald eagles *(Haliaeetus leucocephalus)* was seen in the vicinity and it is considered likely that one or both of them had killed the geese.

INFERTILITY

Infertility was the cause of 9.1 percent of all egg failures. Of all eggs of known history 1.8 percent were infertile. Occurrence of losses due to infertility was erratic.

DEATH OF THE EMBRYO

Losses due to the death of the embryo may usefully be classified according to their occurrence during early or late stages of development. In 36 out of 41 losses caused by death of the embryo, death took place in the first three or the last three days of incubation.

Losses considered to be the result of death of the embryo during early stages of development were 4.2 percent of all losses, accounting for 0.8 percent of all eggs of known history. The cause or causes of such losses under natural conditions is unknown. It might be speculated that in the early part of the incubation period there is a differential ability among embryos to survive any adverse environmental conditions, such as excessive cold or precipitation, which might affect the clutch during temporary absences of the incubating female.

Losses which were the result of death of the well developed embryo were 6.8 percent of all losses, accounting for 25 eggs or 1.3 percent of all eggs of known history.

In 18 eggs well developed young were found to have died apparently because they were in positions such that they could not break out of the shell. These cases of malposition involved the head and beak being directed in such a position that it was impossible for the hatching bird to crack open the egg. Losses due to this cause occurred more often as several in a clutch than as one per clutch. If one can assume that the environment is effectively uniform for all eggs in each nest (the fact that the eggs are regularly turned supports this assumption) it seems reasonable to conclude from the above observations that the factor causing malposition of the embryo is not environmental, but is inherent in the individual egg and is known to occur in related eggs. In other words, there is justification for suspecting a genetic cause.

FLOODING

None of the nests located on the island study areas was destroyed by rising flood water. However, flooding was a substantial cause of loss of nests built on muskrat lodges in Columbia Valley marshes.

DISCUSSION

Figure 2 is an attempt to portray graphically the inter-relationship and relative effectiveness of factors influencing the reproduction of Canada Geese. The central portion of the figure represents the population, and the spaces between the inner circles indicate the relative trends of population status, that is to say, decreasing,

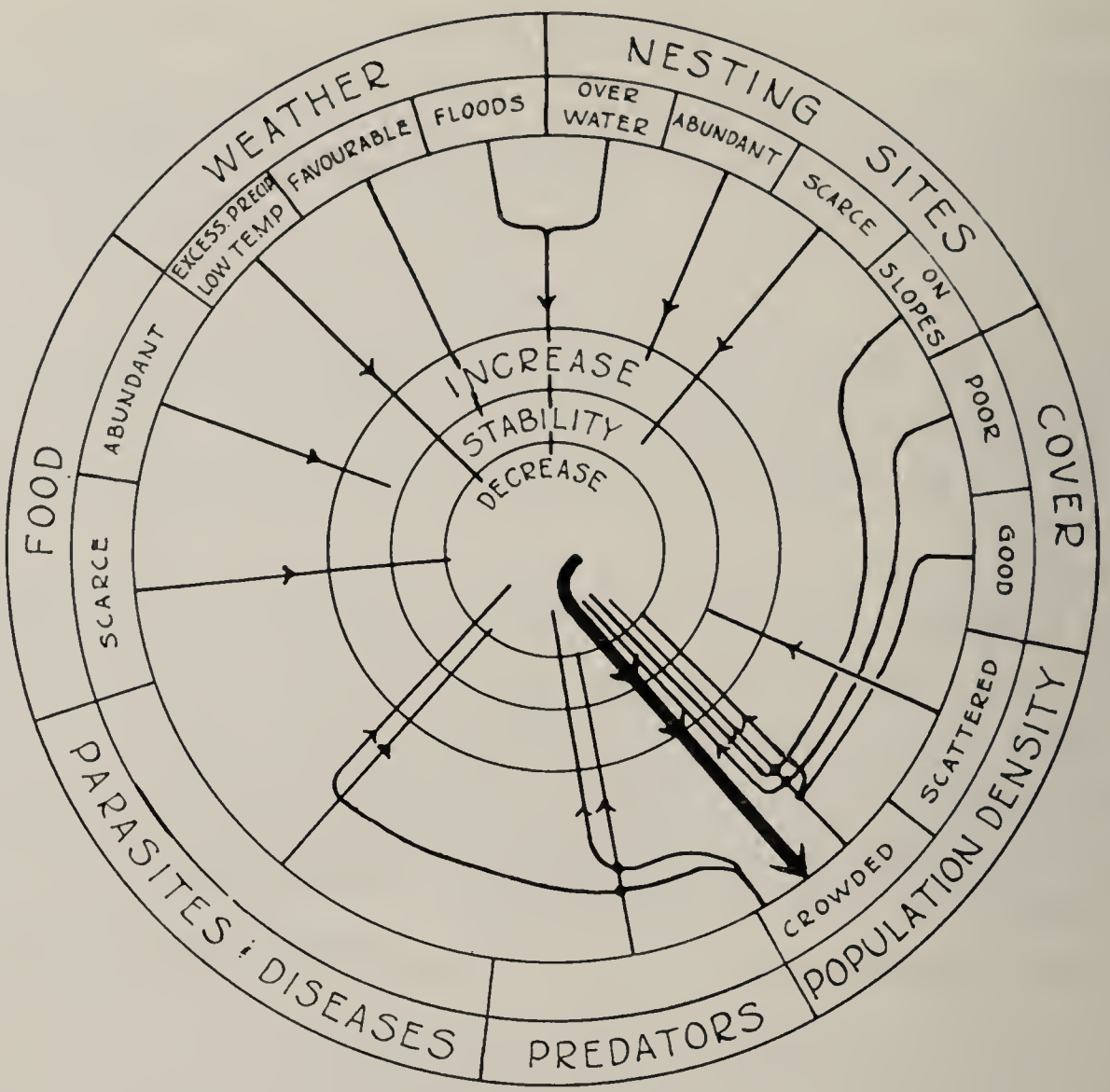

Fig. 2.

stable, or increasing. The compartments around the outer part of the figure represent various factors that may affect the population and the lines running toward the center of the figure indicate how the population may be affected, that is to say, whether it will be increased or decreased. The depths of penetration of the centrally directed lines suggest relative intensities of effects particularly as they may be modified by inter-relationships of factors as shown by linked lines. The heavy line running outward from the center of the figure toward »crowded» represents the biotic potential of the species — its inherent tendency to increase its numbers in the absence of effective reducing factors. Much of the diagram is self-explanatory, but attention should be directed to some of the relationships indicated. The nature of the habitat and of water conditions determines whether or not certain nests will be destroyed by flood waters. If the nature of the habitat is such that it supports a density of breeding geese so high that they nest in close proximity to each other, then it may be expected that there will be intraspecific competition, which has been shown to be a factor having a significant influence on the hatching success of Canada Geese. Another relationship between habitat *per se* and high density resulting from the influence of favourable habitat has been shown. Reference is made to the loss of eggs as a result of intraspecific antagonism from densely crowded nests situated on steep slopes. While it seems evident that nesting geese seldom place their nests in heavy cover,

where good cover exists it may modify the effects of density. This was considered to be the case on Hatfield's Island. Survival of goslings appears to be favoured by the interspersion of dense brushy cover with open feeding areas, such as exists in the upper Columbia Valley.

The effect of weather conditions resulting in floods on nests of Canada Geese located in palustrine habitat has been mentioned. Weather conditions may also affect the success of reproduction in other ways, although evidence of weather effects was not obtained during this study.

Predation has a relatively minor effect on Canada Geese, and no particular pattern of incidence other than the relationship between predation and high density nesting can be obtained from the data at hand. It may be concluded that the Canada Goose is not an important source of food for any predator. Predation on Canada Geese probably occurs only as a result of chance opportunities.

Desertion of the nest was found to be the most important cause of egg loss among the Canada Geese observed. It has been shown that there is a relationship between the incidence of desertion and displacement of eggs from the nest on the one hand and distance between nests or nesting density on the other. In other words, these losses are thought to be to some extent density-dependent. It has been suggested that on Hatfield's Island the effect of nesting density on the rate of desertion may be inhibited by the presence of superior cover. It was also suggested that analysis of the density effect, when the phenomenon occurs in an insular habitat surrounded by palustrine habitat, may be complicated because of unmeasurable interaction between birds occupying the two areas. That was thought to be the case at Goose Island.

Having considered the inter-relationships and immediate effectiveness of some of the factors affecting reproduction of Canada Geese, especially in the early stages, it remains of interest to determine the importance of these factors as they may affect the long-term status of a particular goose population. To do so, it is first necessary to establish the characteristics of a theoretically stable population.

A mean hatch of 4.0 was derived from data obtained during the study of 378 clutches. It will therefore be assumed that the average annual production of newly-hatched young is 4.0 per breeding pair in a theoretically stable population.

Annual survival rates of geese are known only for populations wintering in the Mississippi Valley. HANSON and SMITH (1950) calculated annual survival rates varying from 48.0 to 62.7 percent, for different years and from different groups of recovery records of banded birds. They considered the »most accurate survival index for three years of adult life after banding was 60.7 percent». The rate of survival during the first year of life is always less than in succeeding years, and for that critical period HANSON and SMITH calculated the rate at 34.6 percent.

The age of attainment of maturity has not been satisfactorily defined and indeed may be rather variable. Captive Canada Geese generally breed for the first time when they are three years old and sometimes not until they are four. The most useful information on this point is also given by HANSON and SMITH (1950). Evidence from

banded juveniles recaptured and examined a year later indicated that most of them are likely to have bred as two-year-olds.

Let us now consider what would be the age composition of a population having survival rates of 35 percent in the first year and 60 percent in succeeding years in which each breeding pair produced four young. It will be assumed that there is a stable element of 50 breeding birds. Considering the situation at midsummer there would be 100 young, 35 yearlings, 21 two-year-olds, 12 three-year-olds, 7 four-year-olds, 4 five-year-olds, 2 six-year-olds and one seven-year-old. Now, even if all two-year-old birds are assumed to breed it is apparent that the population described above is a waning one because the sum of the individuals two years old and older is only 47 while the initial breeding population is assumed to be 50.

Among the reproductive characteristics given, first-year mortality is probably most open to question. Let us then consider what would be the age composition of a population having the same characteristics as the one described above except that survival rate in the first year is 40 percent. Again assume that there is to be a stable element of 50 breeding birds. At midsummer there would be 100 young, 40 yearlings, 24 two-year-olds, 14 three-year-olds, 8 four-year-olds, 5 five-year-olds, 3 six-year-olds, 2 seven-year-olds and one eight-year-old. If all two-year-olds are assumed to breed, the population described above would be an increasing one because the sum of the individuals two years old and older is 57 while the initial breeding population is assumed to be 50. What is more likely to be generally the case is that only some of the two-year-olds are sexually mature. So, if it is assumed that 70 percent of two-year-olds breed, that average production of young per breeding pair is 4.0, and that survival rates are 40 percent in the first year and 60 percent in succeeding years, a model of a theoretically stable population can be constructed.

Starting again with 50 breeding birds, the age composition of such a population at midsummer would be the same as that given immediately above but the breeding component would be made up of 17 two-year-olds instead of 24 and all the birds older than two years of age. Expressed in percentages, the age classes in a theoretically stable population would be as follows: young, 50.7 percent; yearlings, 20.3 percent; two-year-olds, 12.2 percent; three-year-olds, 7.1 percent; four-year-olds, 4 percent; five-year-olds, 2.5 percent; six-year-olds, 1.5 percent; seven-year-olds, 1 percent; and eight-year-olds, 0.5 percent.

While a population having exactly the characteristics now established might rarely be found in nature, this representation of the age composition and reproductive state of a Canada Goose population is considered to be a useful starting point for demonstration of the effectiveness of factors affecting the early stages of reproduction on the long-term status of populations.

In construction of a population model demonstrating the effect of reduced production of young (Table 4) it is assumed that in Years 0 and 1 the average production of young by an otherwise stable population is reduced from 4.0 to 3.3. This is an approximation of the situation on Hatfield's Island, where the mean hatch was 3.54

TABLE 4

Population Model Showing Results of Reduced Productivity
(3.3 young per breeding pr. for Years 0 and 1.)

Year	0	1	2	3	4	5	6	7	8	9
Breeding birds	50	50	47	45	46	47	48	48	49	49
Young	83	83	94	90	92	94	96	96	98	98
Yearlings	40	33	33	38	36	37	38	38	38	39
All 2-yr. olds	24	24	20	20	23	21	22	23	23	23
Breeding										
2 yr. olds	17	17	14	14	16	15	16	16	16	16
3 yr. olds	14	14	12	12	12	14	13	13	14	14
4 yr. olds	8	8	8	8	7	7	8	8	8	8
5 yr. olds	5	5	5	5	5	5	5	5	5	5
6 yr. olds	3	3	3	3	3	3	3	3	3	3
7 yr. olds	2	2	2	2	2	2	2	2	2	2
8 yr. olds	1	1	1	1	1	1	1	1	1	1

in 1952 and 3.31 in 1953. Had there been no desertion in those years, mean hatches might have been 4.26 and 4.16. Except, of course, for the number of young produced, the age distribution of the population in Year 0 is assumed to be that which has been set up for a stable population. In Year 1 there is a similar age distribution, except that again the number of young produced is lower than average and the number of yearlings is lower because of the reduced production of young in Year 0. In Year 2, production of young per breeding pair is returned to normal but there is a reduction in the breeding population resulting from the reduction in the two-year-old element. In Year 3, reduced production of young in Years 0 and 1 has its greatest effect on the size of the breeding population. Recovery in the size of the breeding population commences in Year 4 and proceeds slowly until Year 9 by which time it is virtually complete.

TABLE 5

Population Model Showing Results of Increased Productivity
(4.8 young per breeding pr. for Years 0 and 1.)

Year	0	1	2	3	4	5	6	7	8	9
Breeding birds	50	50	54	57	56	57	58	58	59	60
Young	120	120	108	114	112	114	116	116	118	120
Yearlings	40	48	48	43	45	45	45	46	46	47
All 2 yr. olds	24	24	29	29	26	27	27	27	28	28
Breeding										
2 yr. olds	17	17	21	21	18	19	19	19	20	20
3 yr. olds	14	14	14	17	17	16	16	16	16	17
4 yr. olds	8	8	8	8	10	10	10	10	10	10
5 yr. olds	5	5	5	5	5	6	6	6	6	6
6 yr. olds	3	3	3	3	3	3	4	4	4	4
7 yr. olds	2	2	2	2	2	2	2	2	2	2
8 yr. olds	1	1	1	1	1	1	1	1	1	1

In construction of a population model demonstrating the effect of increased production of young (Table 5) it is assumed that in Years 0 and 1 the average production of young by an otherwise stable population is increased from 4.0 to 4.8 The mean hatch of the Goose Island population in 1953, when losses due to desertion were negligible, was 4.8. Again, except for the number of young produced the age distribution of the population in Year 0 is assumed to be that which has been set up for a stable population. In Year 1 there is an increased number of young and of yearlings. An increase in the breeding population is first noted in Year 2, and the trend continues even while production per breeding pair is at the average level until Year 9, when stability is obtained at an increased population level.

Changes in production of young such as have been demonstrated in these two population models thus can be seen to have potentially significant effects on population status. However, because of the interactions of factors influencing other stages in the life history of the species they can rarely be clearly discerned in nature.

Factors reducing the early reproductive success of Canada Goose populations may from time to time cause temporary decreases in numbers, and these may be of considerable magnitude if they should happen to coincide with reduced survival during autumn and winter. It seems evident, however, that so long as there are no significant changes in habitat, the compensatory effect of increased average production of young by populations of low density can bring about population recovery.

Factors increasing the early reproductive success of Canada Geese may cause temporary gains in populations within the areas which they traditionally occupy. Every area, however, has its carrying capacity, which may be limited by the amount of food present, the availability of nesting sites, the extent of suitable rearing areas, and other environmental factors on the one hand or by the degree of intraspecific tolerance on the other. In the case of the Canada Geese on Hatfield's Island and Goose Island it seems evident that population increases are checked by a reduced average production of young, which occurs when the level of intraspecific intolerance is reached.

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Über die Ausbreitung und Verbreitungsgrenze der Türkentaube *Streptopelia decaocto* (Friv.) in Osteuropa

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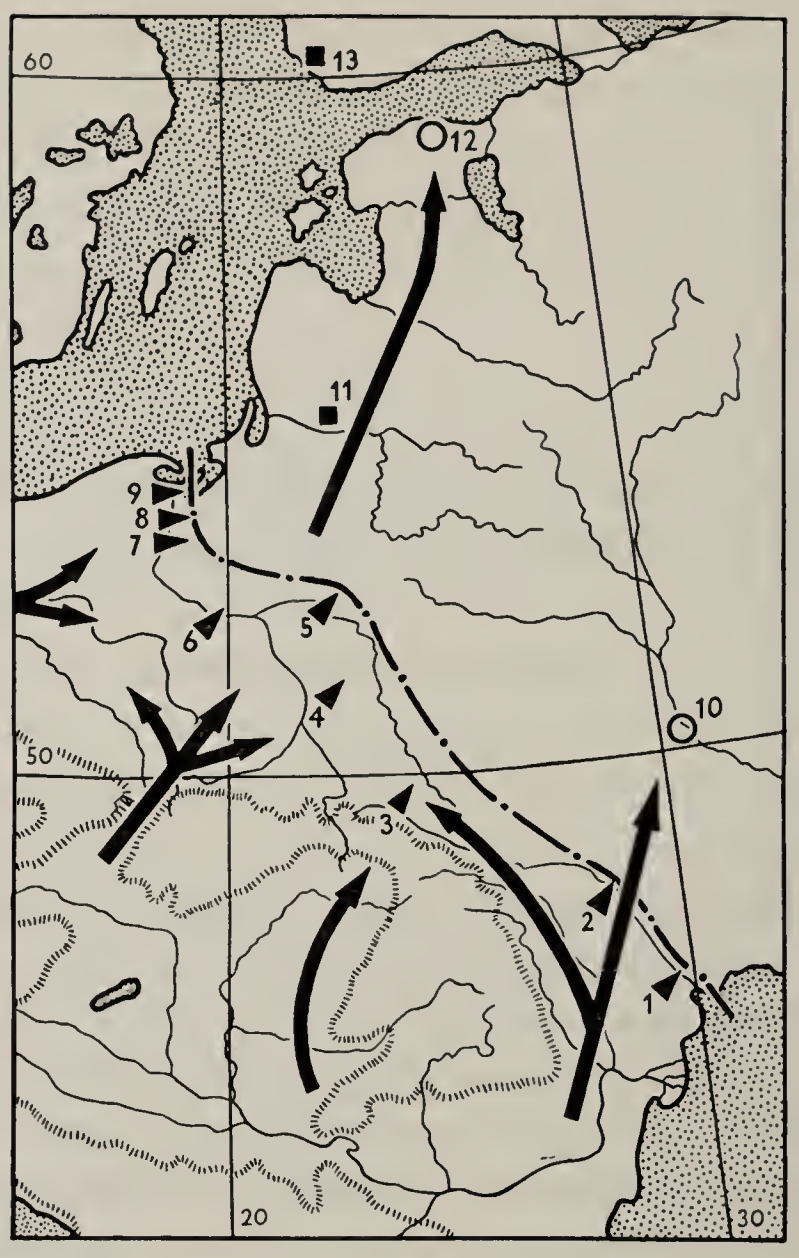
Warszawa

Vor 24 Jahren, während des VIII. Internationalen Ornithologenkongresses in Oxford, berichtete der ungarische Ornithologe Geno Nagy über die ersten Ausbreitungschritte der Türkentaube in Ungarn. Heute ist der Vogel in fast ganz Europa bekannt und gilt den Tiergeographen als eines der extremsten Beispiele rascher Ausbreitung. Aus dem bis jetzt vorliegenden Material geht hervor, dass die Ausbreitung vom Balkan aus hauptsächlich nach dem Nord-Westen Europas gerichtet ist. Die Türkentaube hat sich aber auch schon in weit östlich gelegenen Orten als die in Balkan gelegener Brutpunkte angesiedelt, sich also nicht nur nach dem Norden und Westen, sondern auch nach dem Osten Europas ausgebreitet, in dieser Richtung aber in relativ langsamem Tempo. Während sie in ganz Europa in ca. 30 Jahren (1928—1957) im Durchschnitt fast 60.000 qkm/Jahr besiedelt hat, wurden im Osten Europas (vom 20. Längengrad zählend) nicht ganze 20.000 qkm/Jahr in Besitz genommen. Das dürfte damit zusammenhängen, dass die Temperaturen im Osten Europas im Durchschnitt bedeutend niedriger sind als im Westen; auch die menschliche Siedlungsweise ist in den östlichen Ländern über weite Strecken eine andere; die Dauer des Sommers und Herbstes ist hier kürzer.

Die Ungarische Tiefebene, die Ebenen Rumäniens und die Slovakei besiedelte die Türkentaube vor dem Jahre 1950, sich direkt vom Balkan her ausbreitend. Nachdem sie in Ungarn schon sehr häufig war, ist sie in Siebenbürgen langsam eingedrungen. Hinter die Karpaten ist sie wahrscheinlich auf folgenden Wegen gekommen (Karte 1): aus dem östlichen Bulgarien, entlang dem Schwarzen Meer, die Ostkarpaten vermeidend nach Bessarabien, Moldavien bis zur Ukraine; aus der Tschechoslovakei durch die Mährische Pforte nach Südpolen; aus Sachsen, der Mark Brandenburg und Meklenburg nach Nord- und Mittel-Polen; Prof. Strautman aus Lwow schrieb mir (2.8.57), dass das Eindringen dieser Vogelart in die Gegend von Lwow (Galizien) auch aus der Slovakei und der hinterkarpatischen Ukraine durch die hier niedrigen Karpaten möglich ist.



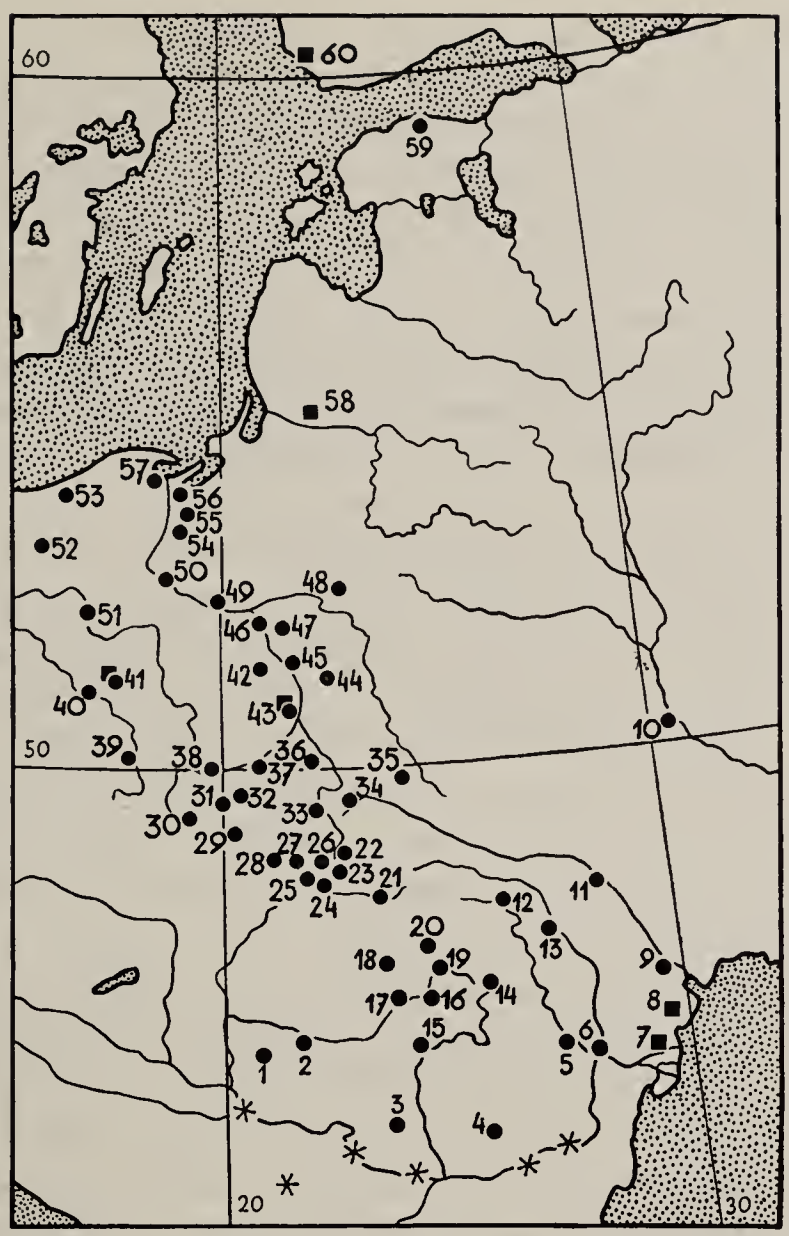
Karte 1. Allgemeine Ausbreitungswege und Verbreitungsgrenzen der Türkentaube in Osteuropa. Pfeile = vermutliche Ausbreitungsrichtungen vom Balkan aus; ▶ = Grenzbrutvorkommenspunkte; ○ = isolierte Areale; ■ = Vorkommen einzelner, nicht brütender Vögel. — Weitere Erläuterungen im Text.

Die Ansiedlungen der Türkentaube in den Tälern der Flüsse Weichsel, San, Dnjestr und Pruth waren die Ausgangspunkte zu der weiteren, noch heute vor sich gehenden Ausbreitung dieses Vogels weiter nach dem Norden und Osten Europas.

Materialien über die Ausbreitung und Verbreitung der Türkentaube

Die Brutplätze in Ungarn, Mähren und Böhmen, schon längst bekannt, sind nicht berücksichtigt; angegeben sind hier nur Stellen in Rumänien, der östlichen Slovakei, der Ukraine, die wichtigsten Stellen in Polen, Litauen, Estland und Finnland. Unten verzeichnete Angaben habe ich chronologisch angeordnet. Die in Klammern angegebenen Zahlen verweisen auf Punkte der Karte 2.

1833: **1** (8) *Tatarbunary*, NORDMANN 1838: einige Paare beobachtet, davon 1 Paar erlegt. — **2** (7) *Kilia*, NORDMANN 1838: im Sommer 1 Ex. erlegt. Angeblich sollte sich dieses von der Türkei nach Bessarabien verflogen haben. (Es ist sehr wahrscheinlich, dass diese Taube hier von den Türken eingeführt wurde, die bis 1812 in Bessarabien herschten. Nach Abzug der Türken aus diesem Gebiet hat sich die künstlich angesiedelte Population verkleinert, (die restlichen Vögel traf noch Nordmann 1833), später ist sie vollkommen verschwunden. Erst im 20. Jahrhundert brachte der natürliche Ausbreitungsdrang diesen Vogel wieder nach Bessarabien).



Karte 2. Neuansiedlungen der Türkentaube in Osteuropa in den Jahren 1932—1957; auch Beobachtungen aus dem Jahre 1833.

● = neue Brutansiedlungen; ■ = Vorkommen einzelner, nicht brütender Vögel; ★ = nördlichste Vorkommenspunkte vor Beginn der Ausbreitung. — Weitere Erläuterungen im Text.

1932: **3** (17) *Aiud* (= *Nagyenyed*), Jacobi briefl. 8. 5. 57: 1 Paar brütet seit mindestens 1932.

1936: **4** (1) *Timisoara* (= *Temesvár*), Radu 1957: Ansiedlung.

1938: **5** (5) *Bukarest*, Radu 1957: Ansiedlung.

1939: **6** (9) *Neu Borodino*, Heer 1950: 1 Brutpaar mit Nest und 2 Jungen gefunden.

1940: **7** (3) *Craiova*, Radu 1957: Ansiedlung — **8** (2) *Lipova* (= *Lippa*), Radu 1957: Ansiedlung — **9** (41) *Olesnica* (= *Oels*), Wirries 1949: Ausnahmsweise 1 Ex. in Gesellschaft von 2 Turteltauben 2.5 km von der Stadt entfernt angetroffen.

1941: **10** (43) *Radoszki b. Sandomierz*, Nowak 1958: Ausnehmsweise wurden Türkentauben beobachtet. Es ist möglich, dass die Vögel von den deutschen Ansiedlern aus Bessarabien gebracht wurden.[1]

1942: **11** (20) *Besztercze* (= *Bisztriz*), Haltrich briefl. 14. 10. 57: Es ist anzunehmen, das die Türkentaube schon 1942 hier heimisch war. 1943 4—6 Ex. gesichtet.

1943: **12** (27) *Michalovce*, Cerny briefl. 10. 1. 57; Ferianc 1946: Brutvorkommen.

1944: **13** (6) *Galati* (= *Galatz*), Frank 1948: Im Sommer gesichtet — **14** (23) *Mukatschewo* (= *Munkács*), Strautman briefl. 2. 7. 57: Nach brieflicher Mitteilung schon 1944 brütend — **15** (26)

[1] Wie mir Herr E. Heer aus Bopfingen, früher in Bessarabien, mitteilte, war es den deutschen Umsiedler nicht möglich, lebende Tiere nach Polen mitzunehmen. Die Tauben in Radoszki können also nur vom Süden her zugewandert sein.

Ushgorod (= *Ungvár*), STRAUTMAN 1947; 1953: 3 Brutpaare beobachtete A. A. Grabar. Während des schweren Winters 1946/47 fast alle umgekommen. 1952 wieder häufig.

1945: **16** (37) *Tarnów*, NOWAK 1958: Brut festgestellt; später Vermehrung — **17** (39) *Glubczyce* (= *Leobschütz*), NOWAK 1958: 1 Brutpaar beobachtet; vielleicht nistete sie schon früher.

1946: **18** (24) *Beregowo* (= *Beregszász*), STRAUTMAN 1947: Brut festgestellt — **19** (28) *Kosice* (= *Kaschau*), CERNY br. 10. 1. 57; FERIANC 1946: Brut festgestellt.

1947: **20** (15) *Sibiu* (= *Hermannstadt*), JACOBI briefl. 8. 5. 57: Mehrere Brutpaare; Ansiedlung wahrscheinlich früher; 1952 mindestens 50—70 Brutpaare; 1953 dagegen auffällig wenig — **21** (38) *Kraków*, NOWAK 1958: Erste Sichtung im Winter 1945. Später vereinzelte Stücke beobachtet; ab Frühjahr 1947 vergrösserte sich der Bestand ständig.

1948: **22** (35) *Lwow* (= *Lwów* = *Lemberg*), STRAUTMAN 1951; 1954; briefl. 2. 7. 57: Nach brieflicher Mitteilung hat die Taube 1948 hier gebrütet; auch 1949 und in weiteren Jahren. Im Winter 1950 bei —25° überstand ein Teil die Fröste — **23** (40) *Wroclaw* (= *Breslau*), DYRCZ 1956: Brut festgestellt; es ist möglich, dass sie schon 1947 in der Stadt sesshaft war.

1949: **24** (5) *Focsani*, KOHL 1954: Gesichtet — **25** (16) *Marosvásárhely* (= *Tirgu Mures* = *Neumark*), MANNSBERG 1950: 1 Paar im Sommer beobachtet — **26** (18) *Kolozsvár* (= *Cluj* = *Klausenburg*), MANNSBERG 1950: 1 Paar im Sommer beobachtet — **27** (21) *Tjatschew* (= *Técsö*), STRAUTMAN 1953, *Chust* (= *Hüszt*) u. *Winogradow* (= *Nagy — Schölös*), STRAUTMAN 1951: Ansiedlung — **28** (25) *Tschop* (= *Csop*), STRAUTMAN 1951: Ansiedlung — **29** (34) *Sambor*, STRAUTMAN 1951: 1. August wurde rufender Tauber gehört.

1950: **30** (30) *Liptovsky Mikulás*, CERNY briefl. 10. 1. 57: Brut festgestellt; dieser Ort liegt im Váh (= Wag) — Tal in der Tatra, zwischen Bergpässen von etwa 2.000 m Höhe — **31** (43) *Radoszki b. Sandomierz*, NOWAK 1958: 1941 beobachtet, dann 1948; 1950 Brut festgestellt.

1951: **32** (19) *Szászregen*, KOHL 1954: 2 Brutpaare; später häufig — **33** (32) *Stary Sacz*, NOWAK 1958: Brut; im Herbst schon 13 Stück beobachtet, davon einige gefangen und in den Wroclaw-Zoo gesandt — **34** (36) *Sokolów Mlp.*, NOWAK 1958: Brut festgestellt; Dezember 1954 ca 30 St. beobachtet — **35** (42) *Radom*, NOWAK 1958: Brut festgestellt — **36** (50) *Torun* (= *Thorn*), NOWAK 1958: 1950 gesichtet; ab 1951 Brut und ständige Vermehrung festgestellt — **37** (51) *Poznan*, MICZYNSKI 1951; NOWAK 1958: Gesichtet 1950; 1951 Brut festgestellt — **38** (52) *Stargard Szczecinski* (= *Stargard*), NOWAK 1958: Brut festgestellt; starke Vermehrung.

1952: **39** (13) *Jassy* (*Iasi*), RADU 1957: Ansiedlung — **40** (22) *Swaljawa*, STRAUTMAN 1953: Häufige Vorkommen — **41** (29) *Huncovce, Strázky, Velka Lomnica*, BETHLENFALVY 1953: Ansiedlung in den drei genannten Gemeinden im Poprad Tal in der Tatra, zwischen Bergpässen bis 2.000 m Höhe — **42** (31) *Nowy Targ*, NOWAK 1958: Vermehrung ab 1952, 1953 sehr häufig; im Winter 1953/54 erfroren die meisten — **43** (33) *Bazanówka b. Sanok*, M. SOKOLOWSKI briefl. 16. 4. 58: in Garten Brut festgestellt — **44** (41) *Olesnica* (= *Oels*), DYRCZ 1956; NOWAK 1958: Brut festgestellt; Ansiedlung erfolgte nach Angaben hiesiger Bewohner viel früher — **45** (53) *Lekowo Krs. Bialogard* (= *Belgard*), NOWAK 1958: Brut festgestellt; 1953 6 Ex. beobachtet — **46** (58) *Taurage*, IVANAUSKAS 1957: Ausnahmsweise 1 Ex. am 27. 7. 52 erlegt.

1953: **47** (45) *Pulawy*, NOWAK 1958: Brut festgestellt — **48** (46) *Warszawa*, NOWAK 1958: Im Zoo (rechts der Weichsel) Brut festgestellt; in späteren Jahren häufig an verschiedenen Stellen — **49** (49) *Plock*, NOWAK 1958: Brut festgestellt — **50** (56) *Marynowy b. Nowy Dwór Gdanski* (= *Tiegenhof*), M. SOKOLOWSKI briefl. 16. 4. 58: seit 1953 brüten regelmässig mehrere Paare — **51** (60) *Askainen*, v. HAARTMAN 1955: 11.—12. 6. 53 1 Ex. beobachtet.

1954: **52** (44) *Lublin*, DYRCZ 1956; NOWAK 1958: Brut festgestellt; gesichtet ein paar Jahre früher.

1955: **53** (14) *Ciuc u. Gyimespass*, JACOBI briefl. 8. 5. 57: Vereinzelte Brutpaare in Parkanlagen; diese beiden Ortschaften liegen in den kältestens Gegenden Siebenbürgens — **54** (12) *Botosani*, RADU 1957: Ansiedlung — **55** (10) *Kiew*, KISTIAKOWSKIJ 1957: Brut festgestellt; in den nächsten Jahren Vermehrung; 1958 mehrere Brutpaare briefl. 25. 4. 58 — **56** (54) *Kwidzyn* (= Marien-

werder), Nowak 1958: Brut festgestellt — **57** (57) *Gdansk* (= *Danzig*), Nowak 1958: Brut festgestellt.

1956: **58** (11) *Soroki*, Nasarenko briefl. 25. 6. 57: Ansiedlung — **59** (47) *Minsk Mazowiecki*, Nowak 1958: Brut festgestellt; seit 1953 beobachtet — **60** (48) *Wysokie Mazowieckie*, Swiderski br. 26. 4. 58: Zahlreich im Sommer beobachtet; es ist anzunehmen, dass die Taube hier brütet; auch 1957 zahlreich gesichtet.

1957: **61** (55) *Malbork* (= *Marienburg*), Dyrcz 1956; Nowak 1958: Brut festgestellt; einzelne Exemplare schon im Winter 1953/54 gesichtet — **62** (59) *Kostivere* (= *Kastifer*) *b. Tallin*, Kumari briefl. 10. 3. 58: 1 Brutpaar festgestellt; die Entfernung von den nächsten Brutorten in Polen beträgt in Luftlinie 700 km (Gdansk), oder 750 km (Wysokie Mazowieckie).

Provisorisch kann man also die Vorkommensgrenze der Türkentaube in Osteuropa durch folgende Orte ziehen (Karte 1): Neu Borodino (1), Soroki (2), Lwow (3), Lublin (4), Wysokie Mazowieckie (5), Plock (6), Kwidzyn (7), Malbork (8) und Marynowy (9). Ausserdem sind aber isolierte Vorkommen dieser Taube in Kiew (10) in der Ukraine, in Kostivere bei Tallin (12) in Estland und ein einziges Exemplar aus Taurage (11) in Litauen und auch nur eines aus Askainen (13) in Finnland bekannt Wie bei der Ausbreitung dieser Taube im Westen Europas festgestellt ist — (wo die neuen Fundorte mit manchmal übertriebener Genauigkeit durch die Fachzeitschriften registriert wurden), haben oft gleiche Vorsprünge die breite Ausbreitungsfront überholt (z. B. Pattensen in Deutschland, Brutansiedlung in Grafschaft Moray-Elginshire in England u. a.).

Ich habe briefliche Nachrichten aus Weisrussland (Golduschko 14. 4. 58; Siershain 8. 5. 58), dass die Türkentaube dort bis jetzt nicht beobachtet wurde. Auch in Odessa am Schwarzen Meer kommt sie als Brutvogel bis jetzt nicht vor (Nasarenko briefl. 25. 6. 57). Da aber noch immer neue Nachrichten über die Ausbreitung dieser Taube aus dem Osten Europas kommen, und da das Areal jetzt nicht geschlossen ist, muss man annehmen, dass die Ausbreitung hier noch weiter vor sich gehen wird.

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Lipid Deposition in Nocturnal Migrant Birds

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In our ecological studies at the University of Georgia we are particularly interested in the relationship between primary productivity (the rate of energy fixation by photosynthetic and chemosynthetic organisms) and assimilation by consumer organisms. The fat or lipid content of populations is of considerable interest in this connection since fat is often the most variable of the large components of biomass and is worth, energetically speaking, over twice as much per gram as other organic components. Seasonal and other changes in fat levels, therefore, may serve as indicators of certain aspects of the metabolic status of populations. In the present paper we shall be concerned with the actual amount of fat carried by migrating birds and its use as fuel during flight; we are not here concerned with the ecological and physiological mechanisms bringing about the storage of fat prior to migration.

The ability of migratory birds to store and utilize large amounts of fat has been known in a general way for a long time but we seem to have been the first to determine by actual extraction the total amount of fat in wild birds under various seasonal and experimental conditions (Odum and Perkinson, 1951; Odum and Connell, 1956; Odum and Major, 1956; Odum, 1958). While changes in weight of marked captive or wild birds as well as the superficial appearance of sub-cutaneous deposits can serve as useful indices of relative fatness, the absolute quantity of fat must be known if the energy available for migratory flight is to be estimated. The data in this report deal with a particularly interesting sample of nocturnal migrants killed by striking a tall television tower during the 1956 autumn (southward) migration. As may be seen from the map in Figure 1 the television tower is located on the Gulf of Mexico coast along one of the important routes for birds migrating from eastern North America to winter ranges in Central and South America. Birds reaching the vicinity of the tower have, as it were, three choices; they can (1) terminate the flight in the vicinity, (2) continue along the coast eastward or westward, or (3) continue non-stop over the 500 or more miles of open water to Yucatan or other points in Mexico. Lowery (1946) has presented evidence indicating that many individuals of many species of small land birds do indeed undertake the long over-water flight.

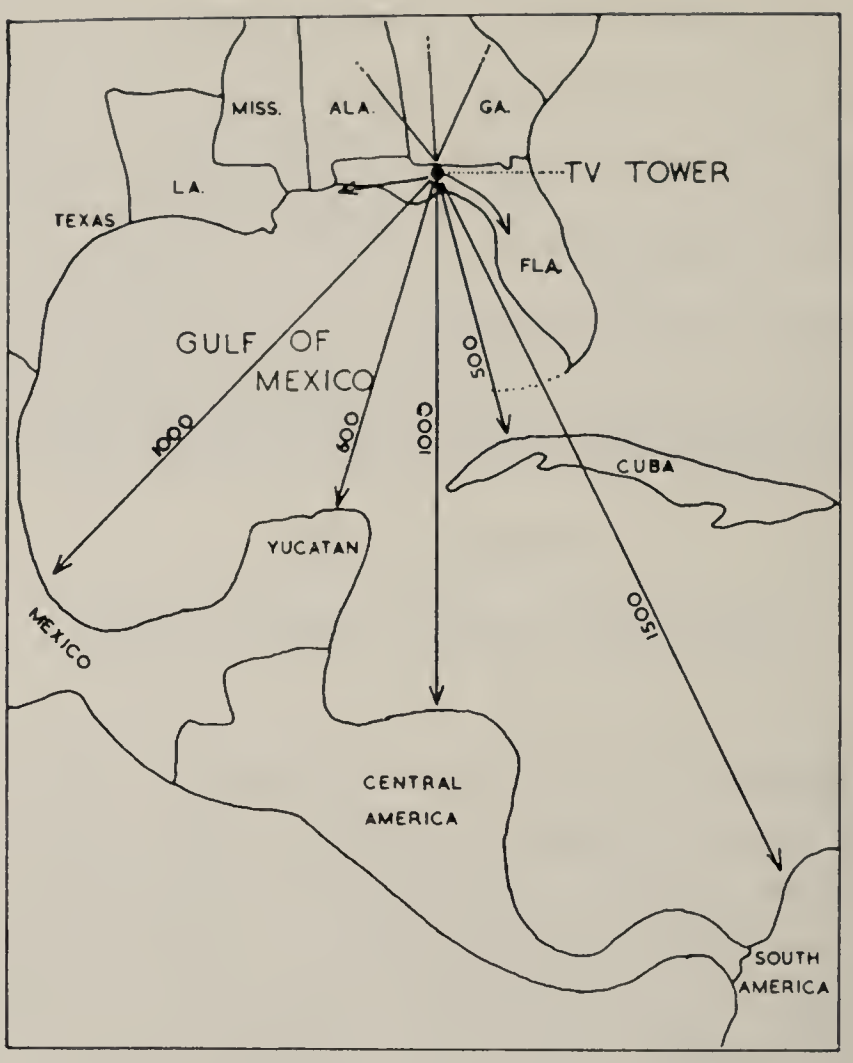

Fig. 1. Sketch map of the Gulf of Mexico region showing location of the television tower at which samples of migrating birds were obtained. Arrows indicate possible routes and the minimum over-water distances in miles between the tower and wintering ranges.

While we have no way of knowing what the birds would have done had they not struck the tower and become part of our study samples, the results of our lipid analyses do provide a firm basis for estimating possible flight range beyond the point where they were killed.

These studies were made possible by Mr. HERBERT L. STODDARD of Thomasville, Georgia, who obtained the specimens killed at the tower. Laboratory extraction of lipids was carried out by Mr. CLYDE E. CONNELL assisted by Mr. SMITH KIMBALL, Miss GUTHRIE TOLBERT and Mr. LESLIE DAVENPORT.

METHODS

Birds were collected at the base of the tower throughout the autumn migration period (August to December) of 1956, and placed immediately into deep-freeze. Mr. STODDARD who lives near the tower visited the site at daybreak every morning, collected all the birds killed the previous night, and kept a complete record of the total kill. To facilitate the easy location of fallen birds he arranged to have the grass under the tower mowed, and he also regularly applied insecticide to prevent ants and other insects from attacking the specimens. We were thus provided with a unique »frozen bird museum» of specimens all in excellent condition; only a small part of this collection has so far been analysed.

To facilitate the rapid processing of large numbers of specimens a more rapid method of extraction was devised than that employed in our previous work (ODUM and CONNELL 1956). After weighing, sexing and aging (by skull ossification) the frozen carcass was ground up in a

chilled meat chopper and placed in a vacuum drying oven. When completely dry the material was weighed on an analytical balance and extracted in petroleum ether over a steam bath (or as an alternate procedure allowed to remain in cold ether solution followed by final warming over the steam bath). The residue was then dried again and weighed. The difference between the first and second weight gives the water content of the specimen, the difference between the second and third weight the lipid content, and the final weight represents the non-fat dry weight. While extraction by this rapid method is not quite as complete as that obtained by the use of successive lipid solvents in the standard Soxlet or Bailey-Walker apparatus (as used in our previous work) the time saved enabled us to process larger numbers of specimens and thereby obtain a better estimate of population levels. Actually, the small percentage of lipid remaining in the final residue probably represents tissue lipids, and is partly compensated for by non-lipid material which dissolves out in the ether solution. In any event the values listed in this paper certainly represent the maximum amount of available fuel which the bird could use in flight.

The names and winter ranges (as given in the 1957 edition of the American Ornithologists Union Checklist) of the ten species discussed in this paper are as follows:

Porzana carolina (Linn.). Sora Rail. Winters from southern United States, south through Mexico, Central America and West Indies to Colombia, Peru, Venezuela, Trinidad and British Guinea.

Vireo olivaceus. Red-eyed Vireo. Winters in the Amazon Basin from southeastern Colombia, Eastern Ecuador and southwestern Venezuela to eastern Peru and western Brazil. Migrates across Gulf of Mexico to Yucatan and thru central America to N.W. South America. Also thru southern Florida, Fla Keys, Western Cuba and Isle of Pines.

Vermivora peregrina (Wilson). Tennessee Warbler. Winters from Guerrero, Oaxaca, and Guatemala south to Colombia and northern Venezuela.

Dendroica magnolia (Wilson). Magnolia Warbler. Winters from S.E. San Luis Potosi, Puebla, central Veracruz, Tabasco, Yucatan and Quintana Roo thru Central America, to Costa Rica and Panama; and in Bahamas, Cuba, Isle Pines, Jamaica, Hispaniola & Puerto Rico. Casual in winter in Sonora, Miss. & Fla.

Dendroica castanea (Wilson). Bay-breasted Warbler. Winters from Central and eastern Panama to northern Colombia, Western Venezuela; transient in eastern Mexico and eastern Central America.

Dolichonyx oryzivorus (Linn.). Bobolink. Winters in eastern Bolivia, Western Brazil, Paraguay and northern Argentine — in migration thru Mississippi valley (chiefly in spring), Atlantic coastal states, Fla, across Gulf of Mexico and Caribbean Sea and thru West Indies.

Piranga olivacea (Gmelin). Scarlet Tanager. Winters from N.W. & C. Colombia south thru Ecuador to central Peru and central western Boliva. In migration thru Yucatan, Quintana Roo, Cuba and Bahamas.

Piranga rubra (Linn.). Summer Tanager. Winters from Southern Baja California and Veracruz south thru Mexico and Central America to South central Peru, Western Bolivia, west-central Brazil and Western British Guiana.

Zonotrichia albicollis (Gmelin). Winters chiefly in southeastern United States south to northern Florida and southern Texas.

Passerina cyanea (Linn.). Indigo bunting. Winters from Jalisco, San Luis Potosi, Cuba, Bahamas and Jamaica south thruout southern Mexico and Central America to Central Panama; casually to northern Venezuela; rarely north to Texas, Mississippi, Florida and Bermuda.

The *Vireo* and *Piranga rubra* are common nesting birds in the vicinity of the tower as well as further northward, while the breeding range of *Passerina cyanea* extend southward almost to the tower locality. The other seven species nest considerably to the north and are found in the tower locality during the spring and autumn migration periods (and in winter in the case of *Zonotrichia*).

RESULTS

1. *Lipid Levels.* — *Vireo olivaceous*, which is one of the commonest breeding birds in woodlands throughout eastern North America, occurred in the samples from late August to the end of October. This species proved to be the most variable in fat content, some individuals being as lean as the average non-migrating bird (4—6 % fat) and other individuals approaching maximum levels (40 % fat). In table 1 the average, range and coefficient of variation of the weight of fat, dry non-fat, and water are given for a representative sample of 42 vireos illustrating the range in absolute amounts of major body components which may be expected in migrating birds. The weight of fat varied from less than one to 11 grams per individual bird, while non-fat and water components were much less variable. That is to say, the fat-free or basic weight (water plus non-fat, — about 15 grams in the vireo) was relatively constant, and this proved to be the case in all the other species as well. So far we have not been able to demonstrate that either the water content or the non-fat dry weight is different in a fat bird as compared with a lean one of the same sex, age and species. We note some small differences, especially in water content, which may prove significant when still larger samples have been extracted. However, differences in the non-fat components appear to result mostly from differences in the overall size of individuals.

TABLE 1

Average, Extremes, and Coefficient of Variation (V) for Weight in Grams of Three Body Components of 42 Migrating Vireos Killed at the TV Tower

	Average	Extremes	Coeff. of variation (V)
Total lipids.....	5.73	0.63—11.02	52.4
Dry non-lipids	4.81	4.24— 5.92	8.2
Water	10.35	9.03—12.52	13.3

If fat is expressed as a percentage of either the total wet weight or the total dry weight no difference has been detected between first year individuals (as identified by incompletely ossified skulls) and adults or between males and females. Absence of age or sex differences in the degree of fatness at a specific point along the route is perhaps only to be expected since, in general, pronounced age or sex differences in the length of the migration undertaken have not been demonstrated for the species here considered (even though the seasonal timing may be different in some cases). As would be expected in the autumn first year birds outnumbered the adults in the samples of all of the species.

The results of lipid determinations on 308 individuals of the ten species are shown in Table 2 and in Figure 2. Total lipids in grams and total lipids as a percentage of both wet and dry weight of the whole bird are summarized in Table 2. Since there was no apparent difference in the levels of the three species of warblers *(Parulidae)* the data for these are combined. In *Dolichonyx* and to a lesser extent in *Vireo* the

pattern of lipid deposition was different in early as compared with late migrants; in these species, therefore, two values are given.

In all cases the coefficient of variation for total lipids as a percentage of dry weight was less than that for total lipids expressed as a percentage of wet weight. This suggests, as already indicated, that water content may vary with the degree of fatness, but there is also the possibility of a small but variable dehydration of specimens prior to extraction even though every effort was made to prevent this. In any event it is clear that per cent of dry weight provides the best »fat index». However, since we are concerned in this paper with the use of fat as fuel in migratory flight the wet weight index (that is, lipids as a percentage of the live weight) has more meaning since the bird must transport its water as well as its fat. Consequently, the data are plotted in Figure 2 according to the wet weight index.

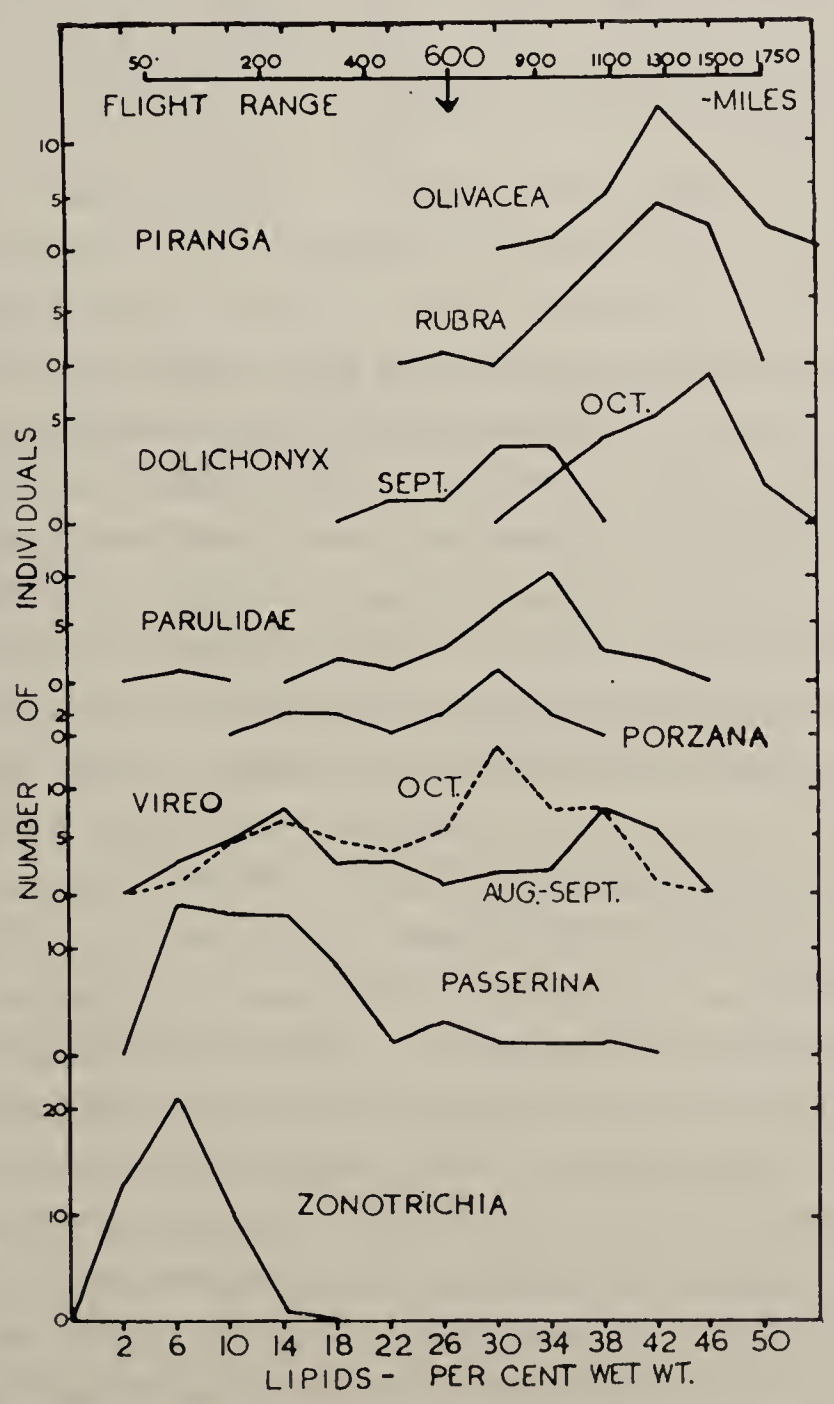

Fig. 2. Frequency distribution of the fat indices (% lipids of total wet weight) of samples of migrating birds killed while in nocturnal flight at the television tower on the west Florida Gulf coast. See text and table 3 for explanation of the flight range scale drawn along the top of the graph.

As shown in Figure 2 a plot of frequency distributions brings out the very striking species differences in the pattern of lipid deposition in birds which were literally »snatched from the air» while in nocturnal migration. The bell-shaped curves of the samples of *Zonotrichia, Piranga* (both species) and *Dolichonyx* suggest that the entire

TABLE 2

Total Lipids of Birds Killed at the Gulf Coast Television Tower during the 1956 Autumn Migration

Species	Period	No. Ind.	Total Lipids Gms.	% Wet Wt.	V*	% Dry Wt.	V*
Zonotrichia albicollis	Oct. 26—Dec. 23	45	1.45	6.22 ± 0.42	45	16.57 ± 1.00	40
Passerina cyanea	Sept. 23—Oct. 9	55	2.00	13.45 ± 0.97	53	31.03 ± 1.66	40
Vireo olivaceus	Aug.—Sept.	41	5.40	24.28 ± 2.03	54	47.04 ± 2.87	39
	October	59	5.58	25.95 ± 1.25	37	51.09 ± 1.45	24
Porzana carolina	Sept. 30—Oct. 30	8	19.86	27.60 ± 2.92	30	51.69 ± 3.57	20
Parulidae (3 species)	Sept. 6—Nov. 4	29	3.72	30.12 ± 1.53	27	55.17 ± 2.03	20
Dolichonyx oryziv.	Sept. 8—16	8	10.25	29.75 ± 1.54	15	54.53 ± 1.68	9
	Sept. 29—Oct. 8	19	17.50	42.02 ± 0.98	10	68.21 ± 0.84	5
Piranga rubra	Oct. 4—5	44	16.61	40.72 ± 0.65	11	66.51 ± 0.58	6
Piranga olivacea	Oct. 4—5	29	17.62	42.64 ± 0.73	9	68.08 ± 0.60	5

* Coefficient of variation

migrating populations of these species were at a uniform fat level. In the case of *Zonotrichia* the entire sample (consisting of individuals obtained during a two month period) was lean, the frequency distribution being similar to that of non-migratory *Passer domesticus* in the autumn. Since the tower locality is near the southern edge of the wintering range of *Zonotrichia* (the center of the wintering range is actually in the Carolinas considerably north of the Gulf Coast) it is to be expected that individuals would be in a »post-migratory» fat condition, that is, not capable of flying much further. It is perhaps noteworthy that a large portion of individuals of this species had less that 4 % fat, which is less than that usually found in non-migrating birds, indicating that fat deposits may indeed be used up during migration (for additional discussion of the situation in this species see Odum, 1958).

In sharp contrast to the situation in *Zonotrichia, Piranga* and *Dolichronyx* were uniformly very fat; these species, of course, winter south of the Gulf of Mexico, and it is quite clear that all individuals killed at the tower would have been capable of continuing flight for a long period in so far as fuel reserves were concerned. In fact, the October *Dolichonyx* and the *Piranga olivacea* were the fattest birds yet encountered, being even fatter (taking in consideration size-metabolism relations) than the hummingbirds about which we previously reported (Odum and Connell, 1956). Percentagewise, the fattest individuals we have yet extracted were two immature male *Piranga olivacea* and one adult male *Dolichonyx*; half (50 %) of wet weight and nearly three-fourths (73 %) of dry weight of these individuals was fat. The September *Dolichonyx* were at a distinctly lower level than the October flight of the same

species (see Fig. 2) but still quite fat. It is noteworthy that *Dolichonyx* has one of the longest migration routes of any land bird since it breeds in northern North America and winters south of the equator.

Frequency distributions of the other species shown in Figure 2 tend to be skewed or bimodal. Thus, most individuals of the *Parulidae* and *Porzana* were quite fat but a few individuals were lean or only moderately fat. Most individuals of *Passerina* were relatively lean but there were a few fat individuals. Distribution was strikingly bimodal in *Vireo olivaceus*, especially in August and September, when most birds were either quite fat or quite lean; later in the season there were more birds at an intermediate level. Since this species is reported to have two widely separated migration routes, one across the Gulf and the other via peninsular Florida and the West Indies, it is possible that the »fat» population would have flown directly across the open water, while the leaner population would have gone the other way where there is ample opportunity for stopping to refuel in southern Florida. However, it should be emphasized that any such suggestion is mere speculation; large samples from the 1957 migration now being studied may clarify the evidently complex situation in this species.

2. *Estimation of Flight Range.* — Since the general energy requirements for muscular work in warm-blooded animals are well known the information we now have on the actual fat levels may be used to estimate possible flight ranges of the nocturnal migrant birds. There seems no longer any doubt that lipid deposits are used by flying birds, and that the fat is more readily available as a source of muscle energy than was formerly supposed (see George and Naik, 1958). In fact, there is now physiological evidence to support the idea that »migratory fat» is, unlike the inert fat masses of obese human beings, a temporary organ with its own enzyme systems and other mechanisms which facilitate rapid utilization. Therefore, we shall assume that the time aloft and the non-stop distance which can be flown under a given wind condition depends largely on the energy content of the »migratory fat body».

While no one has yet measured the rate of metabolism of a migrating bird it is quite logical to assume that the energy needed for migratory flight is, in a relative way, comparable to that required in other types of sustained hard work. By its very nature long distance migration must be strenuous, but not exhausting in the sense that fatigue develops to the point of stopping the work before the energy reserves are depleted. Therefore, we might expect that a migrating bird, a horse which works hard all day, and a cross country runner or hiker who is able to keep up a sustained pace all day would have similar energy requirements relative to the basal level. While the rate of metabolism, of course, varies greatly in different species, and especially in different sizes, of animals, the ratio between the energy required for general maintainance of the body and that required for different work levels seems to be quite similar for large and small homeotherms. Brody (1945) reports that the ratio of sustained work energy to basal metabolism is from 3 to 8 in man, horses and cattle.

Since moderate work, such as walking, requires something over twice the basal energy level, then the ratio of hard work to moderate work energy is from 2 to 4. These ratios are based on actual measurements of the rate of metabolism of animals and man at different work levels. A similar ratio is obtained when we consider the well-known daily caloric requirements of man since 1,700 Kilo-Calories are required for basal metabolism, 3,000 for moderate work and 6,000 for hard labor. In other words for man and domestic animals the ratio of hard, sustained work to moderate work (as is required for ordinary daily existence) is from 2 to 4.

The excellent data of PEARSON (1950, 1954), who has measured the rate of metabolism of hummingbirds at different work levels, indicate that the same general ratios hold for small birds as well as for horses and men. The Kilo-Calories per gram of bird per hour at three work levels are recorded by PEARSON as follows: resting, — 0.066; daytime activity in the field, — 0.17; hovering flight — 0.40. The daily requirement was estimated by observing the amount of time hummingbirds spent in various activities (feeding, resting, flying, etc.) out-of-doors and calculating energy needs from laboratory measurements of energy required at different work levels. From these data we see that the ratio of flying (strenuous, sustained activity) to resting is 6 and the ratio of flying to the moderate activity of a resident wild bird is 2.35. Thus, although the rate of metabolism per gram biomass in hummingbirds is high, and even though hovering flight may be more strenuous than migratory flight, it is evident that the ratio between energy required for everyday life and that required for sustained, strenuous work is of the same order of magnitude in horses and hummingbirds.

KENDEIGH (1949) has termed the energy expended at the moderate work level as »existence energy» since this is the energy required by a bird for food gathering and general survival at a given air temperature when no energy is being expended for breeding, migration, or other strenuous activity. Existence energy has been frequently estimated for species of the genera *Passer, Zonotrichia, Junco, Fringilla, Parus* and others by keeping birds in cages (where they are free to hop and fly about, feed, etc.) and determining the metabolizable energy content of the food consumed per unit of time (see KENDEIGH, 1944, 1949; SEIBERT, 1949; KING and FARNER, 1956; ODUM and MAJOR, 1956; GIBB, 1957; RAUTENBERG, 1957). These studies indicate that approximately one Kilo-Calorie per bird per hour is required for a 20—25 gram bird which is not undergoing fat deposition or otherwise subjected to energy demands beyond that required for day-to-day existence. Since, in this paper, we are dealing with birds whose weight may be greatly increased by large fat deposits (which in themselves do not have as great a rate of metabolism per gram as the non-fat tissue) it is best to consider existence energy in terms of the lean or fat-free weight. Therefore, we may accept 0.05 K-Cal/gram fat-free weight/hour as a reasonable figure for existence energy requirements of birds whose fat-free weight is between 10 and 30 grams. All but one species here considered falls within this range. For *Porzana*, which has a fat-free weight of about 50 grams, existence

energy per gram is probably less (according to the inverse size-metabolism principle); in the absence of actual data we can only suggest 0.04 K-Cal/gram/hour as an estimation. Below 10 grams body size becomes especially critical; in very small hummingbirds daytime existence energy is several times greater (see PEARSON's listed data), but the 24 hour average may be considerably reduced by the ability of hummingbirds to become partly poikilothermic at night. In our subsequent consideration of energy demands during migration we shall ignore the metabolism of the fat body itself (which is apparently small), but we shall make allowances for the energy needed to transport the extra fuel (as we have seen a 20 gram bird (fat-free-weight) may have up to 20 grams of potential fuel »on board«!).

Possible flight ranges, that is, distances beyond the tower which the birds might have flown without stopping to feed, are estimated in Tables 3 and 4. Calculations are somewhat different in the two tables, but both estimates are based on the well-established figures for existence metabolism of small birds and on the assumption that the energy needed for sustained flight would likely be at least two times, but not more than four times, the existence energy. In table 3 various possibilities are shown for a bird with a fat-free weight of 20 grams and with from 1 to 20 additional grams of fat (the range actually found in migrating birds of this size; see table 2). The available energy for flight is calculated assuming that one-half gram of body fat is not available. This assumption is based on the fact that several individuals of *Zonotrichia, Passerina* and *Vireo* were down to about this much, but no individual had less than this amount. Three different estimates of flight range are given (the last three columns table 3) on the assumption that ratio of flight energy to existence energy might be 2, 3 or 4 as previously discussed. Thus, if existence energy is 1 K-Cal/bird/hour, then the energy needed for sustained flight might be 2, 3, or 4 K-Cal/bird/hour. If the average flight speed is 30 miles per hour (there is much evidence to indicate that a 20-gram bird can maintain air speed for long periods without fatigue) then the energy cost per mile would be 0.067, 0.1, and 0.133 K-Cal. respectively. It is probable that variations in air speed (that is, speed independent of effect of winds as contrasted to ground speed which may be greatly affected by tail or head winds) are not critical in these estimates as long as the bird remains within its capable range for sustained flight since BRODY (1945) has shown that the energy cost per mile for walking in man is independent of the speed of walking. Thus, if the bird flies faster than 30 miles/hour it will complete the journey faster but the energy cost per hour will likely be greater leaving the cost per mile roughly the same.

All things considered it would seem that the flight ranges as based on the ratio of 3 (next to last column, Table 3) represent reasonable and conservative estimates for migratory flight under average conditions. Where favored by tail winds the ranges in the »2« column might be expected, while ranges in the »4« column might represent adverse although not exhausting conditions. Any energy expenditure rate beyond 4 times existence levels would presumably be exhausting, if continued for long, and result in the bird being forced down.

TABLE 3

Available Energy and Estimated Flight Range at Different Fat Levels for a Migrating Bird with a Fat-free Weight of 20 Grams

Total Wet Wt	Total Lipids Gms.	Total Lipids % Wet Wt.	Available Energy Gms. fat	Available Energy K-Calories	Flight Range in Miles Assuming Flight Energy (in K-Cal) per mile is 0.067*	0.1*	0.133*
21	1	4	0.5	4.5	68	45	34
23	3	13	2.5	22.5	337	225	169
25	5	20	4.5	40.5	607	405	304
27	7	26	6.5	58.5	877	585	437
30	10	33	9.5	85.5	1282	835	640
33	13	39	12.5	112.5	1687	1125	844
35	15	43	14.5	130.5	1956	1305	978
37	17	46	16.5	148.5	2225	1485	1114
40	20	50	19.5	175.5	3630	1755	1316

* factors in the three columns are based on assumption that flight energy/existence energy is 2, 3 and 4 respectively; see text for explanation.

TABLE 4

Estimated Flight Range of Migrating Populations at the Time that the Samples Were Killed at the Gulf Coast TV Tower

Migrating Population		Fat-free Weight, gms.	Existence Energy, K-Cal/bird/hour	Available Flight Energy gms.	Available Flight Energy K-Cal	Flight Range*, Miles
Zonotrichia		21.6	1.08	0.9	8.1	75
Passerina	lean group	12.9	0.64	1.2	10.8	169
	fat group	12.9	0.64	3.3	29.7	465
Vireo	lean group	15.2	0.76	1.6	14.4	190
	Mod. fat group	15.2	0.76	6.0	54.0	710
	fat group	15.2	0.76	8.5	76.5	1070
Porzana	Mod. fat group	50.1	2.5	7.6	68.4	274
	fat group	50.1	2.5	21.9	197.1	787
Parulidae		9.4	0.47	3.3	29.7	632
Dolichonyx,	Sept. group	24.0	1.2	9.2	82.8	690
	October group	24.0	1.2	16.5	148.5	1237
Piranga rubra		24.0	1.2	15.6	140.4	1170
Piranga olivacea		23.5	1.17	16.6	149.4	1278

* based on ratio of flight energy/existence energy = 3 and an average speed of 30 miles/hour; see text for explanation.

If we consider the flight range in relation to the »fat index», that is lipids as a percentage of wet weight (column 3), the data in Table 3 may be used to estimate the flight range not only of a 20-gram bird but of any small bird with a fat-free weight within the range considered in this paper. Accordingly, a scale of flight range based on the ratio of flight energy/existence energy = 3 has been drawn along the top of the graph in Figure 2. Since the minimum over-water distance between the Gulf coast and Yucatan (see Fig. 1), the presumed »trans-Gulf» route for many small

birds, is 600 miles (1,080 kilometers) an arrow has been placed at this point on the scale so that one may estimate at a glance the portion of the various populations capable of a nonstop flight of 600 or more miles. In table 4 existence energy is calculated separately for each species on the basis of the fat-free weight and the factors 0.05 and 0.04 K-Cal./gram/hour as previously discussed; then, flight range is calculated for the ratio of 3 as was done in Table 3. Where the frequency curves show more than one distinct peak (see Fig. 2) average flight ranges are calculated for groups of individuals represented by each peak. Thus, the three distinct peaks in the *Vireo* curve can be used to separate out three populations, namely, the »lean», the »moderately fat» and the »fat». Estimates in Table 4 are quite similar to those obtained by the use of the generalized data in table 3.

Tables 3 and 4, as well as the flight range scale in Figure 2, indicate that practically all individuals in the samples of *Piranga* and *Dolichonyx* and most of the individual *Parulidae* and *Porzana* would have been able to continue non-stop across the open water of the Gulf from the point where they met sudden death by crashing into the tower. In general, one might suggest that any small bird otherwise in good condition which has a wet weight fat index of 27 or greater should be able to make a trans-Gulf flight without difficulty. A large number of individuals in our samples had an index much higher than this suggesting a considerable margin of safety. In fact, most of the tanagers and October bobolinks could probably have flown on to Central America (1,000 miles or 1,800 kilometers) and some of the individuals could probably have reached the South American coast (1,500 miles or 2,700 kilometers) without stopping.

These long potential flights are of interest in connection with the phenomena of the »coastal hiatus» as reported by Lowery (1945) for the spring migration. Since transients which winter in the tropics are usually scarce in spring along the Gulf coast during good weather but abundant during bad weather, it has been suggested that the birds do not alight at the first landfall but continue flying northward so long as the weather is favorable. If we assume that lipid deposition is as great in the spring as in the fall (see Odum and Connell, 1956, for data on lipid levels in spring migrants) then the estimates in Table 4 certainly indicate that many birds carry enough fuel for a flight covering not only the 600 miles of open water but the 200—300 miles of coastal plain as well.

Of the 10 species considered in this paper, at least seven have been recorded by Lowery (1946) aboard ships in the Gulf (that is somewhere between Yucatan and the Gulf coast of the United States) as follows: *Piranga* (species not identified), *Dolichonyx oryzivorus*, *Vireo olivaceus*, *Vermivora peregrina*, *Dendroica magnolia*, *D. castanea*, and *Passerina cyanea*. *Vireo*, *Vermivora* and *D. castanea* were recorded in the autumn migration, the others during the spring migration. As we have seen, the lipid levels in our samples of these species were generally high except for *Passerina*. According to our estimations only about six individuals out of the sample of 55 of the latter species would have been able to continue non-stop across the Gulf;

most individuals would have had to follow the land route or else stop along the coast for extensive re-fueling before attempting the over-water flight.

Quite apart from the question of the over-seas vs the land route it is evident from the data on lipid deposition that a general direct correlation exists between the overall length of the migration route and the degree of fatness. Thus, of nine species wintering chiefly south of the tower, the distance between the breeding range and the winter range (see description of ranges given earlier in this paper) is greatest in *Piranga olivacea* and *Dolichonyx* and least in *Passerina*. *Zonotrichia* has a relatively short migration route which is entirely over land, and, as previously recorded (Odum, 1958), the maximum pre-migratory fat deposition in the spring is only moderate (generally not over 25 % of wet weight).

Perhaps the most interesting result for our lipid determinations has been the demonstration that birds migrating at the same time and place may differ very markedly in the amount of fat present, and that within the same species groups of individuals may exhibit an entirely uniform level (as in *Piranga* or *Zonotrichia*) or several distinctly different levels even when (as in *Vireo)* only one geographic race or subspecies is involved. It will be noted that most of the species herein considered are either not poly-typic, or have only one described morphological race that would be expected in the samples. We shall later report on the situation in species where two or more sub-species are identifyable in the samples.

Summary

Total lipids, non-fat dry weight and water content were determined for 308 individuals of ten species killed during autumn nocturnal migration by striking a tall television tower on the Gulf of Mexico coast of northwest Florida.

Total lipids varied from less than 2 % of wet weight (or 5 % of dry weight) in some individuals of *Zonotrichia albicollis* (a species which does not migrate beyond the Gulf coast) to a maximum of 50 % wet weight (or 73 % dry weight) in some individuals of *Piranga olivacea* and *Dolichonyx oryzivorus* (species which winter at or south of the equator). Non-fat dry weight and water were much less variable, the fat-free weight being essentially constant for a given species, age and sex. Hence a migrating bird with a fat-free weight of 20 grams may have from one to 20 additional grams of fat.

Within each species no difference in fat levels between first year individuals and adults or between males and females was evident, but the number of individuals in these categories was not large enough for definite conclusions in this regard.

Frequency distribution indicated that samples of *Piranga* (two species) and *Dolichonyx* were from homogeneous populations which were uniformily very fat while the sample of *Zonotrichia* was from a uniformily lean population. Frequency curves for the *Parulidae* (three species), and *Porzana carolina* were skewed to the left (most individuals fat, but with a few leaner ones) while that of *Passerina cyanea*

was skewed to the right (most individuals lean, but with a few fat ones). *Vireo olivaceus* was the most variable in % fat, the frequency curve being distinctly bimodal or even trimodal suggesting that two or more populations differing greatly in lipid levels were intermixed in the flights. The October flight of *Dolichonyx* was distinctly fatter than the September flight, while the pattern of fat deposition in late migrant Vireos was somewhat different from the early migrants of the same species.

Possible flight ranges were estimated based on well-established values for existence energy requirements of small birds and on the assumption that the ratio of flight energy to existence energy would likely be greater than two but not greater than four; the latter assumption is based on actual ratios between moderate work and sustained hard work levels in both large and small homeotherms as reported in the literature.

Flight range estimates suggest that any small bird with a wet weight fat index of 27 % or greater could make a non-stop flight under average conditions of at least 600 miles (1,080 kilometers), which is the minimum over-water distance between the Gulf coast and Yucatan, the presumed route of trans-Gulf migrants. Numerous individuals in the samples had a fat index much greater than 27. According to the estimates all individuals of *Piranga* and *Dolichonyx*, most individuals of *Parulidae* and *Porzana*, and about half of the vireos could have easily continued non-stop across the Gulf from the point where they were killed by striking the tower. A large number of individuals in these groups had enough fuel reserves for an estimated flight of 1,000 miles, and some individuals enough for 1,500 or more miles. On the other hand none of the *Zonotrichia* and only a very few individuals in the *Passerina* sample had enough fat for a trans-Gulf flight despite the fact that the winter range of the latter is chiefly on the opposite side of the Gulf.

Quite apart from the question of over-water flights there was a general direct correlation between the length of migration route (that is, distance from breeding to winter range) and the average lipid levels in the species.

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Zur Ökologie der Lappentaucher (*Podiceps cristatus*, *griseigena* und *auritus*) in Estland

S. Onno

Tartu

Das der vorliegenden Übersicht zugrunde liegende Material wurde hauptsächlich in den Jahren 1951—1957 an verschiedenen Gewässern Estlands gesammelt. In der erwähnten Periode nistete der Haubentaucher *Podiceps cristatus* (L.) in Estland an mindestens 112 verschiedenen Stellen und war im Mittel durch insgesamt 775 Paare vertreten. Beim Rothalstaucher *P. griseigena* (Bodd.) waren die Zahlen entsprechend 15 und 100 und beim Ohrentaucher *P. auritus* (L.) 66 und 175. Das Nisten des Schwarzhalstauchers (*P. nigricollis* Brehm.) in Estland konnte bisher nicht nachgewiesen werden, und der Zwergtaucher *P. ruficollis* (Brehm.), der hier in früheren Jahren erwiesenermassen an zwei Stellen genistet hat, ist zur Zeit von unseren Gewässern verschwunden. Somit bezieht sich das obenerwähnte Originalmaterial lediglich auf die drei zuerst genannten Arten.

Auf der Nahrungssuche tauchen Haubentaucher und Rothalstaucher meist serienweise, wobei stets bis 50 Tauchvorgänge rasch aufeinander folgen. Beim Ohrentaucher sind die Serien kürzer (bis 15 Tauchhandlungen), auch kommt es oft zu vereinzelten, durch längere Pausen unterbrochene Tauchakten. Die Tauchdauer hängt bei den Lappentauchern von der Wassertiefe der Tauchstelle ab (nach Angaben von 1 862 Messungen der Tauchdauer). Je tiefer die Tauchstelle, desto länger ist die mittlere Tauchdauer. Von den hier behandelten Lappentaucherarten weist der Rothalstaucher bei gleicher Tauchtiefe die längste und der Ohrentaucher die kürzeste Tauchdauer auf. Unter gleichen Bedingungen sind die Pausen innerhalb einer Tauchserie beim Ohrentaucher am längsten und beim Rothalstaucher am kürzesten. Die maximale Tauchdauer beträgt nach unseren Angaben beim Haubentaucher 50, beim Rothalstaucher 46 und beim Ohrentaucher 31 Sekunden.

Über ihren Nistgewässern fliegen am häufigsten die Ohrentaucher und am wenigsten häufig die Haubentaucher, doch werden von letzteren oft zwecks Nahrungssuche längere Flüge von vielen Nistgewässern zu benachbarten Gewässern unternommen.

Dem Menschen gegenüber ist der Ohrentaucher am zutraulichsten, während der Haubentaucher die meiste Scheu bezeigt. Bei der Gefahr ziehen Hauben- und Rothalstaucher es meist vor, unterzutauchen, während der Ohrentaucher sich fliegend zu retten sucht.

Beim Hauben- wie beim Rothalstaucher lassen sich 6 verschiedene Rufe unterscheiden, die häufig zu feststehenden Kombinationen aneinandergereiht werden, wobei sich Reihenfolge und Anzahl der analogen Elemente in den Lautkombinationen beider Arten ähnlich sind. Der Ohrentaucher zählt in Estland zu den schweigsamen Vögeln, dessen Getriller höchst selten und lediglich im Mai zu hören ist.

Das durchschnittliche Ankunftsdatum der Lappentaucher in Mittel-Estland war im Zeitraum von 1948—1957 für den Haubentaucher der 19. April und für den Ohrentaucher der 28. April. Der zahlreiche Durchzug des Haubentauchers setzt etwa zehn Tage nach Ankunft der ersten Individuen ein und zieht sich, zahlenmässig nachgebend, bis Ende Mai hin. In der ersten Hälfte des Mai ziehen Rothalstaucher und Ohrentaucher in geringer Anzahl durch. Ihre Nistgewässer verlassen die ersten Haubentaucher schon in der zweiten Hälfte des August, der eigentliche Herbstdurchzug beginnt aber erst Mitte September und dauert bis Anfang November an. In manchen Jahren sind einige Individuen noch bis Ende Dezember an unseren Meeresküsten anzutreffen. Im Jahre 1951/52 überwinterten zwei Haubentaucher an der Südküste der Insel Saaremaa. Beim Ohrentaucher beginnt das Verlassen der Nistgewässer schon Ende Juli und setzt sich bis ins zweite Drittel des August fort. Der zahlenmässig schwache Durchzug von Rothals- und Ohrentauchern dauert bis Anfang Oktober an. Die Lappentaucher (insbesondere der Ohrentaucher) ziehen mit Vorliebe zur Nachtzeit, doch auch des Morgens und Abends. Der Haubentaucher zieht, besonders auf dem Frühjahrsdurchzug, in kleineren Verbänden, seltener einzeln. Die beiden anderen Arten wurden überwiegend als Einzeldurchzügler angetroffen.

Die mannigfachsten Balzhandlungen lassen sich beim Haubentaucher beobachten. Die Balz des Rothalstauchers hat mit derjenigen des Haubentauchers 3 Elemente gemeinsam — die Annäherung, das Brust an Brust-Schwimmen und das Nebeneinanderschwimmen. Das Spiel wird stets von lautschallenden Balzrufen begleitet. Im Gegensatz zum Balzgehaben des Haubentauchers fehlt in der Balz des Rothalstauchers gewöhnlich das Tauchen. Die Balz des Ohrentauchers ist noch ärmer an Handlungen und findet sehr selten statt.

Mit dem Nestbau beschäftigen sich die Lappentaucher täglich nur einige Stunden und sie beginnen damit 4—8 Tage vor der Ablage des ersten Eies. Die meisten Lappentauchernester in Estland befinden sich in vorjährigem Röhricht. Weniger als Hauben- und Rothalstaucher ist der Ohrentaucher beim Anlegen seines Nestes an alte Röhrichte angewiesen. Ziemlich häufig wählt der Haubentaucher seinen Nistplatz in überschwemmten Gebüschen. Als Niststoffe verwenden die Lappentaucher sowohl halbverfaultes als auch unverfaultes Material, ohne dem ersteren einen merkbaren Vorzug zu geben.

Kolonienweise nistet vornehmlich der Haubentaucher. In Estland nistet diese Art am Peipussee in einer Kolonie von 50 Paaren und darüber. Kleinere Kolonien sind auch an anderen Seen zu finden. Der Rothalstaucher nistet dagegen stets einzeln. Das Nistrevier des Ohrentauchers ist in der Regel kleiner als das der erstgenannten Arten, weshalb die Nester sich oft ziemlich nahe beieinander befinden. Der koloniale Instinkt scheint aber bei dem Ohrentaucher schwächer ausgebildet zu sein als beim Haubentaucher. In Brutkolonien ist der Eierverlust geringer als in Einzelnestern.

Kolonienweise nisten die Lappentaucher vornehmlich auf Gewässern, die von einer grossen Anzahl von Paaren besiedelt sind. Es ist anzunehmen, dass der koloniale Instinkt sich am stärksten ausgebildet hat gerade bei den Lappentaucherarten, die zahlreich auf einem Gewässer zu nisten pflegen (Hauben- und Schwarzhalstaucher).

Auf vielen Gewässern nisten die Lappentaucher mit Vorliebe inmitten von Möwenkolonien (hauptsächlich von Lachmöwen), wo der Eierverlust kleiner als sonst irgendwo ist. Diese Vorliebe findet sich am ausgeprägtesten beim Haubentaucher, weniger beim Ohrentaucher. Vom Rothalstaucher werden Möwenkolonien als Nistreviere gemieden. Folglich nisten die Arten, die sich gern zu homotypischen Kolonien zusammenschliessen, auch häufiger in Gesellschaft von Möwen.

Oft findet man in nächster Nachbarschaft — mit einem Abstand von nur wenigen Metern — Nester von Blässhühnern *(Fulica atra* L.) und Rothalstauchern oder von Blässhühnern und Haubentauchern. Da wir in den meisten Fällen (28 von 37) feststellen konnten, dass das Blässhuhn zeitiger mit der Eiablage begonnen hatte als der in der Nähe nistende Taucher, hat es den Anschein, dass es der Taucher ist, der die Gesellschaft des Blässhuhnes sucht. Durch dieses Nisten nahe beieinander verengert sich das Nistrevier sowohl des Tauchers als auch des Blässhuhnes. So kann der Abstand zwischen zwei Tauchernestern merklich kürzer sein beim gemeinsamen Nisten mit dem Blässhuhn, als in einem gewöhnlichen Nisten der genannten Taucherarten im nichtkolonialen Nistrevier. Dasselbe ist geltend auch für die Blässhühner, die in der Nähe eines Tauchers nisten. Zwischen Ohrentaucher und Blässhühner kommt es in der Regel zu keiner Nistnachbarschaft.

Die Nistzeit wird von uns durch die Legezeit des ersten Eies charakterisiert (Tabelle 1).

Im Falle gleicher Nistbedingungen auf demselben Gewässer decken sich die

TABELLE 1

Legezeit des ersten Eies bei den P o d i c e p s-Arten in Estland nach Angaben aus den Jahren 1951—1956

Art	Nester-zahl	Mai 1—10 %	Mai 11—20 %	Mai 21—31 %	Juni 1—10 %	Juni 11—20 %	Juni 21—30 %	Juli 1—10 %
P. cristatus	417	3.4	15.8	35.0	31.7	9.8	3.4	0.9
P. griseigena	66	9.1	27.3	44.0	16.6	3.0	—	—
P. auritus	68	2.9	11.8	41.1	29.4	11.8	1.5	1.5

Legezeiten beim Hauben- und Rothalstaucher vollständig. Beim Ohrentaucher setzt die Eiablage auf demselben Gewässer in der Regel eine Woche später ein. An versteckten oder sonstwie bevorzugten Nistplätzen beginnt die Eiablage früher. Beim Haubentaucher gehören vorwiegend überschwemmte Gestrüppe zu solchen begünstigten Nistplätzen.

Die Legezeit weist in den verschiedenen Jahren ganz erhebliche Schwankungen auf, was von der Witterung, dem Wasserstand und der Entwicklung der Wasserpflanzen abhängt. In einem verspäteten Frühjahr (z. B. 1955) wird die Eiablage verzögert und auf eine kürzere Periode zusammengedrängt.

Die Legepause innerhalb eines Geleges beträgt beim Haubentaucher etwa 36 Stunden, schwankt aber beträchtlich. Bei einer täglichen Kontrolle des Geleges um die Mittagszeit wurde festgestellt, dass sich die Anzahl der Eier in vier Haubentauchernestern nach folgendem Schema vergrösserte: 1 — 1 — 2 — 3 — 3 — 4 — 5. Beim Ohrentaucher geschah das in 3 Nestern folgendermassen: 1 — 2 — 3 — 3 — 4 — 5. Die Legepausen betrugen bei der letzteren Art etwa 30 Stunden. Die Eiablage fand zu ganz verschiedenen Stunden am Tage statt.

Eine Zusammenstellung aller aus Estland stammenden Daten über die Grösse der Gelege bei den Lappentauchern ist in Tabelle 2 gegeben.

TABELLE 2

Grösse der Gelege

Art	Zahl der Gelege	Zahl der Eier im Gelege 1 %	2 %	3 %	4 %	5 %	6 %	7 %	8 %	M
P. cristatus	290	—	6.6	25.9	44.8	17.2	4.5	0.7	0.3	3.78
P. griseigena	44	2.3	4.5	45.5	34.1	11.3	2.3	—	—	3.55
P. auritus	63	—	4.7	17.5	33.4	36.5	6.3	—	1.6	4.28

Bei allen der hier behandelten Lappentaucherarten war die mittlere Eierzahl im gleichen Biotop in früheren Gelegen grösser als in späteren. Auch die Jahre, die ein frühes Eierlegen ermöglichten, wiesen eine durchschnittlich grössere Eierzahl auf als die Jahre, in denen die Eierablage sich verzögerte (z. B. das Jahr 1955).

Das Brüten beginnt bei allen hier behandelten Lappentaucherarten sofort nach Ablage des ersten Eies. Beim Rothalstaucher konnte ein mehr oder weniger stetiges Hocken auf dem Nest sogar einige Tage vor dem Legen des ersten Eies beobachtet werden. Während des Anfangsstadiums der Eiablage ist die Bebrütung noch nicht sehr intensiv, und das Nest wird oft freiwillig verlassen, was später selten vorkommt. Die Brutdauer betrug nach unseren Beobachtungen beim Haubentaucher 25 (in einem Falle), 26 (in einem Falle), 27 (3 Fälle) und 29 (1 Fall), beim Rothalstaucher 23 (1), 24 (1) Tage und beim Ohrentaucher 22 (1), 23 (1), 24 (2) und 25 (2) Tage.

In mehreren Lappentauchernestern wurde während einer längeren Abwesenheit der Vögel eine um 1.5° höhere Temperatur festgestellt als in der Umgebung, was durch das Faulen des feuchten Nistmaterials zu erklären wäre. In der Sonne überstieg die Temperatur in den Tauchernestern dank der grossen Wärmeabsorption des

dunkelfarbigen Nistmaterials diejenige der Umgebung sogar bis 6°. Während der Bebrütung ist in den Nestern der Lappentauchern die Temperatur nicht höher als in den Nestern anderer Wasservögel und übersteigt, in einer Tiefe von 1 cm unter den Eiern gemessen, in der Regel nicht 31° C. Dagegen geht das Sinken der Temperatur im Nest, das der brütende Taucher verlassen hat, bedeutend langsamer vonstatten als in den Nestern anderer Wasservögel, und zwar sogar in Fällen, wo die Eier nicht mit dem Nistmaterial zugedeckt waren. Eine Ausnahme bilden starken Winden ausgesetzte Nester, wo die Temperatur rasch sinkt. Dieses langsame Abkühlen ist aller Wahrscheinlichkeit nach durch die grosse Wärmekapazität der feuchten Niststoffe bedingt, welchen demnach beim Nestbau der Lappentaucher biologische Bedeutung zukommt.

Die Pausen zwischen dem Ausschlüpfen der einzelnen Jungen eines Geleges sind weniger konstant als die Legeintervalle. Im Durchschnitt folgen die Ausschlüpfungen einander in etwas schnellerem Tempo als die Ablage einzelner Eier. Daher ist die Brutdauer bei den früheren Eiern etwas länger als bei den späteren.

Die Jungen halten sich während der ersten Lebenswoche zum grössten Teil im Gefieder der Eltern auf, wobei sie häufig von einem der Altvögel zum anderen hinüberwechseln. Den frischgeschlüpften Taucherjungen geht noch die Fähigkeit der Wärmeregulation ab, und der ins Wasser gesetzte Jungvogel erlangt schon im Laufe einiger Minuten eine der Wassertemperatur angenäherte Körperwärme. Dagegen weisen schon ungefähr eine Woche alte Jungvögel im Wasser eine im Vergleich zur Wasserwärme erheblich höhere Körpertemperatur auf, die allerdings die der Altvögel noch nicht erreicht.

In den ersten Tagen ihres Lebens werden die Jungen hauptsächlich vom Weibchen betreut, während das Männchen auf Futtersuche geht.

Obwohl die Eier der Lappentaucher meist bedeckt sind, wird ein grosser Teil von Krähen, Kolkraben und Rohrweihen geraubt, was meist dort geschieht, wo die Vögel durch den störenden Einfluss des Menschen gezwungen sind, ihre Nester im Stich zu lassen. Am stärksten leiden darunter unvollständige und frische Gelege, da solche von den Vögeln oft freiwillig verlassen und nicht sorgfältig genug zugedeckt werden. Durch das Nisten der Taucher in Möwenkolonien wird der Anteil der Raubvögel als Nestplünderer um ein beträchtliches herabgesetzt. An den Meeresküsten werden durch die Brandung vorwiegend Gelege des Haubentauchers vernichtet, doch auch das Trockenliegen der Nester wird daselbst vielen Eiern zum Verhängnis. Ihre Gelege lassen die Lappentaucher nur selten im Stich; am häufigsten geschieht dies in Lachmöwenkolonien. Die Zahl der nicht ausgeschlüpften Eier ist bei den Lappentauchern nicht gross; in 50 untersuchten Nestern fanden sich insgesamt 17 Stück. Davon wurden in nur 5 Nestern Eier späteren Datums mit vollentwickelten Embryonen festgestellt, während es sich in den übrigen Fällen um faule Eier handelte, die sich in der Mehrzahl als die zuerst gelegten erwiesen. Die Sterblichkeit unter den Lappentaucherjungen ist recht gross; aller Wahrscheinlichkeit nach kommt die Hälfte der Jungen ums Leben.

Beim Heraufholen der Nahrung tauchen die Lappentaucher vorzugsweise in offenem Wasser. Vom Rothals- wie auch vom Ohrentaucher werden dabei Gebiete mit Unterwasservegetation bevorzugt. Der Haubentaucher taucht in beliebig tiefem Wasser, zieht aber Stellen vor, wo die Wassertiefe nicht über 5—10 m beträgt. Da der Rothalstaucher in Estland nur solche Gewässer besiedelt, deren Wassertiefe 2.5 m nicht übersteigt, wurde er von uns tiefer tauchend nicht angetroffen. Der Ohrentaucher taucht in der Regel in sehr seichtem Wasser (unter 1 m). Für den Rothalstaucher ist das Tauchen auf einem engbegrenzten Gebiet während eines längeren Zeitraumes bezeichnend. Nach unseren Beobachtungen ist die Nahrungsaufnahme bei den Lappentauchern an keine bestimmte Stunde des Tages gebunden und findet nur um die Mittagszeit etwas weniger häufig statt als zu den anderen Tageszeiten. Im Dunkeln nehmen die Vögel keine Nahrung zu sich.

Zur Bestimmung der Nahrungszusammensetzung wurden die Mageninhalte von 109 Haubentauchern, 45 Rothalstauchern und 56 Ohrentauchern untersucht, wozu das Material vorwiegend im Mai, Juni und Juli eingebracht wurde. Die Hauptnahrung des adulten Haubentauchers bilden Fische, da die Magen der Altvögel zu 89 % (von der Anzahl der untersuchten Magen) Fischnahrung enthielten, während es bei den Jungvögeln zu 39 % der Fall war. Von Fischen bevorzugen die Adultvögel Rotaugen, an manchen Orten aber auch Lauben. Im Mageninhalt der Jungvögel dominieren Flussbarsche. Der Rothalstaucher nährt sich in Estland nur sehr selten von Fischen (in einem Magen waren Überreste des Kleinen Stichlings nachweisbar).

Von allen Lappentauchern werden in grossen Mengen nektonische Arthropoden, vorzugsweise Käfer und deren Larven, Libellenlarven und Wasserspinnen verzehrt, wozu beim Ohrentaucher noch zahlreiche Krebsartige (*Gammarus* u. a.) kommen. Einen beträchtlichen Nahrungsanteil bilden Luftinsekten, insbesondere Schilfkäfer und Libellen.

Zwischen den in den Tauchermagen enthaltenen Federn und der Fischnahrung besteht zweifellos ein Zusammenhang. Die meisten Federn wurden beim Haubentaucher gefunden und die wenigsten beim Ohrentaucher. Das Problem des Federverschlingens hat, unserer Ansicht nach, in der Theorie eine befriedigende Lösung gefunden, nach welcher die Federn dem Vogel als Hilfsmittel bei der Gewöllebildung dienen. Beim Rothalstaucher und beim Ohrentaucher konnte von uns sowohl das Herauswürgen von Gewölleballen als auch das darauffolgende neuerliche Verschlucken einiger grösseren auf dem Wasserspiegel schwimmenden Federn zu wiederholten Malen beobachtet werden.

On Biologically Important Specific Characters

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By way of introduction, I should like to mention that at one time I was in charge of the bird collections of the Zoological Museum of our University for some years. So I claim to have some first-hand experience of taxonomic problems, although my chief interest has been in other branches of zoology. I am fully aware of the immensely valuable work done by systematists and of its importance to general biology. For a long time people, proud of working on »wissenschaftliche Zoologie», gravely underestimated this kind of work and did not grasp the fact that speciation is one of the most fundamental phenomena of life, and that taxonomic research requires real mastership.

However skilfully a species diagnosis may be made, it does not give an answer to the question: »What makes this population a species?» The characters as given in the description may be exhaustive as a tool for determination, but do not generally say very much about the problem: »What are the real differences between this species and related ones?»

The colour characters may, of course, be important as social releasers or may in some cases have selective value, being cryptic. I should, however, like to stress a point briefly touched upon in my lecture on Thursday night: We cannot hope to understand the significance of colour characters fully without knowing how the birds themselves see them. The general statement that the retina of birds is oversensitive to red colours and undersensitive to blue colours, as compared with the colour vision of man, has only a weak foundation in experimental work but is fairly well supported by the known relative dominance of red and orange oil droplets in the cones of diurnal birds. Perhaps you will allow me to mention a crude experiment I once made during field work in Lapland, although not directly related to the role of the colours of the plumage. Now and then I used umbra-reddish glasses in order to get an impression of what the habitats may have looked like to the birds. The effect was not unexpected but still astonishing: the leaves of the deciduous trees and shrubs looked very light, the needles of spruce and pine almost black. The very small leaves of the dwarf birch *Betula nana*, in fact, sparkled like starlets in the bogs, and the most interesting thing, the habitats where the Willow Warbler *(Phyl-*

loscopus trochilus) occurred differed very much more in their physiognomy from the places where it did not breed when viewed with the red glasses than when seen with the unaided eye. Now there are certainly specific differences between the percentages of variously coloured oil droplets, with corresponding differences in filtering effect upon the wave-lengths of light and I think that a reliable statistical investigation of the colour sensitivity in a sufficient number of birds is badly needed. Perhaps I may draw attention to the lecture to be given by Dr. DONNER. Dr. DONNER has also published a paper in which a correlation between the visual acuity of a number of bird species and the lightness of their habitat was clearly demonstrated, the Robin being the species which had the best power of discrimination in weak light. The number of species was, however, small and this type of experimental work should also be extended to a sufficient number of species, taxonomically closely related but differing as to habitat preference.

The way in which the birds move around in the environment where they feed is obviously of paramount importance in determining their capacity to utilize the habitat resources. If, for instance, you skin a number of fringillid birds of about the same size you will probably be struck by the similarity of the carcasses. Nevertheless anatomical differences between the species are responsible for their mode of locomotion, and the mode of locomotion is unquestionably a biologically very important character. The rather few traits used as characteristics in species diagnoses do not in fact have any clear relation to the functionally important ones. The ability of small birds to hang back downwards under twigs is a valuable property, since it gives the birds access to all parts of the food substrate. If the ability of a number of European passerines to search for food in this way is compared with the sum of the lengths of their middle and hind toes, a close correlation is found. The longer the span, the better the capacity. Another close correlation is found between the torque exerted by *Musculus tibialis anticus* and the habit of moving back downwards. The torque is not only dependent upon the strength of the muscle proper but also, and probably generally to a greater extent, upon the length of the ligament, the loop through which the tendon reaches its insertion point on the tarsus, and upon its distance from the joint.

As a third example I want to mention the anatomical difference between jumping and running birds. These chief modes of moving on the ground seem to be a function of at least three anatomical variables: Weight of the bird, relative length of the femur and relative length of the tarsus. Birds that are too heavy cannot proceed by jumping. A relatively long femur and tarsus provide the mechanism needed to produce the impulse necessary for a long jump. I am fully aware of the oversimplification: the motor pattern of the spinal cord is, of course, different in species that show a different mode of locomotion, but the nervous organization is most certainly secondary to the anatomical.

The differences in length just mentioned are extremely small, but may be efficient even if they amount to fractions of millimeters only. This should be very important

from an evolutionary point of view. Speciation must have been easier if very small anatomical changes, probably caused by a correspondingly small genetical reorganization, have been able to augment differences in capacities essential for the utilization of habitat resources. I would like to stress how useful it would be if museums scheduled for their conservators the taking of a few more measures for labelling. For instance, the effective length of the trunk, from the first thoracic vertebra to the pygostyle, the length of the pelvis, the effective length of the femur, the tibia and the tarsus can easily be measured without much anatomical knowledge. The anatomical details affecting the strength of the bill in dealing with food present more difficult problems, as does the functional anatomy of the wing. The effective wing area could easily be measured, however, and would yield, together with the weight of the bird, an important basic characteristic related to the mode of flying. But as a whole, the anatomical adaptations of the hind extremities and of the beak seem to have a much more decisive effect on those functions in which species differ from each other, than adaptations of the flying apparatus. Birds do not, in general, meet obstacles in the air during their daily routine, although a sufficiently high rate of survival during migration may be correlated with an improvement in the anatomy of the wing.

I started with the plumage as the vehicle of those taxonomic characters to which we turn in the first place. As shown by Dr. WALLGREN in his interesting thesis on the physiology of metabolism in the Yellowhammer *(Emberiza citrinella)* and the Ortolan *(Emberiza hortulana)*, a very slight difference in the fluffiness of the plumage can cause a profound difference in temperature tolerance and in the quantitative food requirement, which may result in a great difference in distribution and in behaviour with respect to migration. The same difference in the degree of fluffiness of the plumage can be observed in nature when comparing a Willow Tit *(Parus atricapillus borealis)* and a Marsh Tit *(Parus palustris)*. I think museums could contribute to our understanding of the adaptations of birds to climate by sacrificing a number of specimens for determining the weight of the plumage, especially the soft plumage, in relation to the weight of the large wing and tail feathers. I would also like to address to systematists in charge of museums an appeal that more attention should be paid to the collection of anatomical material of as many species as possible.

Lastly, it is hardly necessary to point out the significance of behaviour patterns as specific characteristics, since this has been stressed by so many outstanding ornithologists and is a fact well known to every field worker.

The Distribution of the Finnish Bird Fauna

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The distribution of the birds of a country, even a small country like Finland, affords far too many and intricate problems to be dealt with in a short lecture. It is my intention to outline some of the main features as an introduction to your visit and your excursions. As a background, I should like to stress certain points. Until quite recently Finland was a very sparsely populated and poor country. In the 1820's a Reverend FELLMAN was the vicar of the northernmost parish in Finland, Utsjoki, which some of you will visit. He was a keen naturalist and ethnographer. His diary and his scientific annotations have been published and make really interesting reading. I remember one of his entries: »This year's mail was brought yesterday». Now things have changed very much, but we still have wide areas not very much disturbed by human activity nor thoroughly explored biologically. In a remote country, science has a tendency to lag behind the general trends of research. Our biologists clung to the natural history stage longer than the biologists of more advanced countries — in fact until »natural history» again came into fashion as ecology and ethology. This has, of course, been a weakness, but as ornithologists we can derive satisfaction from the fact that a comparatively great amount of interest has been devoted to birds.

I called Finland a small country. Geographically, however, Finland is one of the largest countries in Europe. As the extent of Finland is 1,100 km from south to north, the study of the distribution of species and the causes of this distribution may afford results of general interest. On the usual type of small-scale vegetation maps, Finland extends over three main geobotanical zones: the arctic tundra represented by the summits of the hills in Lapland, the northern coniferous zone, or Taiga zone, and in the southern districts the zone of deciduous woods. The tundra zone consists only of a mosaic of small areas above or beyond the tree limit. The southern zone is of an even more incomplete pattern. Only small patches with oak, maple, ash and lime interrupt the pattern of common tree species and of cultivated land. The habitat was certainly more spectacular in South Finland 1,000—2,000 years ago. Fields and meadows have, of course, chiefly been cleared on the richest soils,

once covered by southern plant communities. A deterioration of the climate has, moreover, diminished their ability to compete with the Taiga elements.

The arctic bird fauna of Finland, with species such as *Carduelis hornemanni, Falco rusticolus, Plectrophenax nivalis, Anthus cervinus, Eremophila alpestris, Nyctea scandiaca, Stercorarius longicaudus, Charadrius morinellus, Anser erythropus* and *Clangula hyemalis* is only an impoverished marginal fauna. Many of its species are strongly cyclical, such as, for example, the Ptarmigan, the Snowy Owl and the Long-tailed Skua. The causes are obvious in some cases, for example the raptorial birds and the Skua, which are dependent on cyclically fluctuating small mammals, lemmings and voles. In other cases they are still being debated, an instance being the fluctuations of the Ptarmigan, which is a consumer of the first order, a herbivor, as are the small rodents. The fluctuations concern not only the population density, but also the southern limit of occurrence. In peak years isolated mountain summits, islands in the endless sea of woods and bogs, may be colonized by Skuas and Snowy Owls, whilst in depression years only species with more stable populations, such as *Plectrophenax nivalis* and *Charadrius morinellus,* are found there.

Between the tundra zone and the Taiga zone in its typical form a transition zone is more or less strongly developed. The light, gay mountain birch zone, the *regio subalpina* of northern naturalists, may reach an extent of tens of kilometers in the Northwest. On the isolated hills in Lapland it is quite narrow. The birches have a thorny appearance, somewhat resembling salt steppe bushes. One of the essential features of the zone, the open structure, the free access of light to the ground, the clean, low vegetation between the trees dominated by lichens and low shrubs such as *Empetrum,* is maintained on drier ground through the adjoining 200—300 kilometers of Taiga wood. The bogs extend for miles and miles, enclose the wooded grounds as in a meshwork and contribute to the general openness of the landscape. Here species such as *Pinicola enucleator, Calcarius lapponicus, Parus cinctus, Bombycilla garrulus, Lanius excubitor, Turdus pilaris, Luscinia suecica, Buteo lagopus, Anser fabalis, Numenius phaeopus, Tringa erythropus* and *nebularia* are characteristic, which does not mean that they are the most abundant species. This privilege belongs to species of a rather widespread occurrence in Finland: The Brambling *(Fringilla montifringilla),* breeding in decreasing numbers almost to the southern coastal area, the Willow Warbler *(Phylloscopus trochilus),* which can be heard everywhere where the moisture of the soil provokes the growth of deciduous bushes or trees, the Redstart *(Phoenicurus phoenicurus),* the Wood Pipit *(Anthus trivialis)* and the Willow Tit *(Parus atricapillus borealis).*

The natural, primeval habitats of the coniferous zone are charcterized by one major feature: They consist of only 2 conifers, the spruce *(Picea abies)* and the pine *(Pinus sylvestris).* On drier grounds with a soil of poor nutritional content as well as on drier bogs the pine dominates, on moister ground with a higher productivity level the spruce. The drier the soil, the lighter is the structure of the wood in its climax stage. Even in southern Finland treeless marshes of a few major types inter-

mingle with the woods, especially on the watersheds between the Baltic sea and the White sea and between the Gulf of Finland and the Bay of Bothnia. Even before the arrival of man, the numerous lakes of the central and eastern parts have created a strong edge effect. The majority of STEGMANN's Taiga birds which are represented in our breeding fauna, have extended their range to the Gulf of Bothnia, but a few of them reach their western limit in Finland, as for example *Loxia leucoptera*, *Emberiza rustica* and *pusilla*, *Phylloscopus trochiloides* and *Tarsiger cyanurus*. A greater number of species are more numerous in the northern parts or do not breed at all in the south: *Perisoreus infaustus*, *Carduelis flammea*, *Parus cinctus*, *Picoides tridactylus* and *Lagopus lagopus*.

The western limit is probably chiefly due to the slowness of spread to the once glaciated areas. The thinning of the population towards the south is apparently caused by climatic factors, but perhaps only indirectly, the direct factor being features in the vegetation. Every time I have met with the lovely little Rustic bunting *(Emberiza rustica)* I have been struck by a typical, but not easily defined character of the vegetation which seems to release its choice of territory: There is a typical mixture of spruce of small size and brushwood, on the slowly growing spruces dark lichens are abundant, there is a certain dull colour tone which is not to be found in the more southern and southwestern parts of Finland. I feel convinced that an exact determination of the colour vision of a sufficient number of birds would elucidate much of their habitat preferencies. We should be able to see the landscape as the birds see it.

Now the climax stage was very often destroyed through forest fires caused by lightning before the arrival of man. Burnt areas soon become covered with grass, herbs and in a few years bushes of deciduous trees, chiefly elder and birch, which grow quickly in soil enriched by the ash. The conifers only appear slowly, good seed years occurring at intervals which are longer the farther north we go. Only after a number of decades do the conifers outstrip the deciduous species and attain dominance after a succession of mixed wood stages. This quite natural cycle of forest rejuvenation has been reproduced on a very large scale by man, who used axe and fire as his most powerful implements for preparing the ground for the cultivation of cereals, corn and rye. Mr. VILKUNA, who opened our session, would be able to give you a most interesting lecture on this remarkable agricultural practice, of which the Finns achieved real mastership. Burnbeating was still common everywhere in this country a hundred years ago, disappearing later in eastern Finland than in the western and southwestern parts. Although until recently the human population was very sparse, its influence on the woodland habitats was profound and extended to the remotest parts of the surroundings of farmsteads and villages owing to the extensive practice of burnbeating. The grounds so cultivated were abandoned after a few years, the successional cycle just mentioned started afresh and new areas were burnt. The most important consequence from an ornithologist's point of view was, of course, the creation of habitats for birds belonging to STEGMANN's southwestern group of

biota, birds of the European zone of deciduous woods, such as *Phylloscopus sibilatrix*, *Sylvia borin*, *Hippolais icterina* and *Oriolus oriolus*. In general, the population density was increased, from about 100 pairs/km² in pure coniferous forest of average productivity to about 300 pairs in mixed woodland or deciduous woodland. Even typical Taiga birds profited by the rejuvenation of the vegetation, which resulted in a richer growth of, for example, blueberries and other berries used as food by many birds. A number of bird species typical of the southern deciduous woodland habitats breed farther north in Finland, especially in the eastern parts, than in Sweden, for example *Hippolais icterina*, *Luscinia luscinia* and *Oriolus oriolus*. The primary cause is the south-eastern centre of distribution and perhaps to some extent the retarding influence of the Danish Straits and the southern Baltic sea, but the dominance of secondary deciduous woodlands in eastern Finland has been a factor strongly promoting the northward spread.

Ecologically, the clearing of land for agriculture and as pastures has resulted in an extension of the steppe and desert habitats into the once closed forest region. It has introduced a number of birds wich do not find enough seed in the forest vegetation, which are adapted for moving on the ground and which are ethologically claustrophobic. The Skylark *(Alauda arvensis)*, the Linnet *(Carduelis cannabina)* and the Partridge *(Perdix perdix)* are typical examples. Other species such as the Starling *(Sturnus vulgaris)* are dependent on open spaces for feeding but need higher vegetation for breeding purposes. Lastly, man has created new cliff landscapes in the form of buildings where swallows, Swifts and House Sparrows find breeding places. These facts are, of course, familiar to all ornithologists. In a sense it is more interesting to ask whether these birds used to breed in our natural landscapes. Some birds, such as the Ortolan *(Emberiza hortulana)*, could not breed, of course. The Skylark and the Partridge have been found breeding on small treeless skerries along the coast, where a fairly rich vegetation of grasses and some herbs may occur, especially on islands manured by gulleries. The Skylark breeds regularly on bogs of the »Hochmoor»-type, but in very small numbers. I feel sure that a population of these birds dependent entirely on these habitats could not perpetuate itself. Both the Starling *(Sturnus vulgaris)* and the Jackdaw *(Corvus monedula)* can nest rather far from open fields in hollow trees, but would not find feeding grounds in a northern landscape without human influence. Raptorial birds such as the Kestrel *(Falco tinnunculus)* and the buzzards are often regarded as equally dependent on man-made feeding grounds, but the northern forests are light enough to provide hunting possibilities suited to their manner of moving. Yellowhammers *(Emberiza citrinella)* might always have been able to find new breeding places on burnt areas during the first few years after the fires with a grass and herb vegetation still dominating, but apparently had to be true migrants. The Common Crow was probably able to live during the summer on the shores of eutrophic lakes or along the coast with their colonies of sea birds. The Wagtail *(Motacilla alba)* and the Wheatear *(Oenanthe oenanthe)* are even nowadays quite regular and common inhabitants of shores with

rocks and stones, and the Winchat *(Saxicola rubetra)* breeds on natural marshes. The Swift *(Apus apus)* is a regular breeder in hollow trees in the middle and northern parts of Finland, and the House Martin *(Delichon urbica)* breeds in scattered colonies on cliffs. So even as far north as this country, the number of species absolutely dependent on human culture is smaller than is generally believed, but with regard to the numbers of birds the activity of man has probably caused an increase to approximately double, on an average, and it has caused an extension of the range of very many species. These species are, of course, chiefly southern birds, adapted to the »Kultursteppe» or to man-made park-like wooded landscapes, but the clearing of the forest zone has opened the way for even a few northern birds of the marginal wood zone to extend their breeding areas southwards. Most of you have probably already come across the Fieldfares *(Turdus pilaris)* breeding almost everywhere in the neighbourhood of human dwellings. Originally it was a bird of the light forests near the border of the tundra zone. Our colleagues visiting the Zoological Station of Tvärminne have seen or will see a landscape with features essentially resembling the landscape of the northern light birch and pine woods. Even the Redwing *(Turdus musicus)* has profited from the results of forestry, especially forestry in a primitive form. One will never find a breeding pair in quite closed forest extending over a wide area, but even moderate clearing can create breeding territories. The Greater Shrike *(Lanius excubitor)* has sometimes bred even in southern Finland on large clear cut or burnt forest areas.

It is impossible on this occasion to discuss the waterfowl and limicoles, the fauna of the coasts and the lakes. I should like to stress the interesting manner in which marine and limnic birds meet on the coasts of the Baltic, where the salinity does not exceed 0.5 ‰. On the northern shore of the island of Tvärminne, our Zoological Station, the Crested Grebe and the Eider Duck breed only some hundred meters apart.

Every biologist is aware of the fact that the recent distribution of species is only a momentary status in an ever-changing world. In our bird fauna we find the following main causes of distributional changes. I already outlined the influence of man. The time that has elapsed since the retreat of the ice of the glacial epoch and the establishment of the still prevailing major habitats has been rather short, about 10,000 years. The »Ortstreue», the breeding place conservatism of some birds, has apparently been strong enough to prevent them from spreading quickly enough to colonize all the new areas available. The Crested Tit *(Parus cristatus)* and the Yellow Wagtail *(Motacilla flava)*, the Grouse *(Tetrastes bonasia)* and the Capercaillie *(Tetrao urogallus)* did not breed on the Åland islands in the twenties and early thirties when I studied the bird fauna there. At least as regards the two first-mentioned species, this could not be ascribed to a shortage of suitable breeding grounds. The Crested Tit has in fact colonized the islands during the last 15 years, having traversed some broad stretches of water which formed an obstacle to a bird not inclined to leave the shelter of the woods.

Lastly, we have the swift extension of the range of a number of southern birds during the last 50—75 years, and a corresponding disappearance of northern species from old nesting sites in South Finland, a phenomenon eagerly discussed by Finnish ornithologists. The well-known change of climate, causing a retreat of the glaciers and polar ice, seems to afford a natural and complete explanation. I should like to emphasize, however, that we should be cautious. The modern agricultural and forestry methods have changed the cultivated landscape as well as the woods. The balance between the population density of birds and the habitat factors is very sensitive. As a crude example might be mentioned the extraordinarily rapid reduction in the numbers of Tengmalm's Owl *(Aegolius funereus)*, during my student years the commonest of our owls, which must be a result of the removal of old hollow trees from the forests. The tendency to create forest blocks of the same age may also be a factor detrimlental to some northern bird species. Moreover, we should not forge that the popuatio ns of birds breeding in the North are very much smaller than the populations breeding south of this country. The tendency to expansion must be stronger in the direction S → N than N → S. For a real causal analysis of the distribution of species we need many more studies on physiology and adaptive characters.

The Wintering of Some Waders in W. Cornwall, S. W. England

A. G. Parsons

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Whilst extensions of breeding range of migratory species evoke widespread interest much less attention is given to the wintering of such species outside their usual range.

This short communication gives some data about the wintering in Cornwall of Greenshank, *Tringa nebularia;* Spotted Redshank, *Tringa erythropus;* Green Sandpiper, *Tringa ochropus* and Common Sandpiper, *Tringa hypoleucos;* it is compiled from ten years personal field study.

Cornwall is a peninsula forming the extreme S.W. tip of England: it is 150 kilometres long and is directed like a pointing finger along a N.E.—S.W. axis. In latitude it is just above 50° N and in longitude its mid-point is about 4°40′ W.

There is approximately 500 kilometres of coast, washed on the north and west by the Atlantic Ocean and on the south by the English Channel. In general the temperature variation is moderate giving an almost subtropical climate; many introduced species of palms, ferns and succulents grow and flower readily in the open.

Although the peninsula is quite narrow the climate on the north coast is harsher in winter than that of the south coast.

This may account for the fact that the wintering areas are mainly in relation to the estuaries of the south coast, especially the Truro-Fal rivers.

Certain other species, whose wintering grounds are south of the Mediterranean Sea; *e. g.* Chiffchaff, *Phylloscopus collybita;* remain regularly. Also recent records of Marsh Harrier, *Circus aeruginosus;* Little Gull, *Larus minutus;* and Black-tailed Godwit, *Limosa limosa;* may indicate an increasing trend in this direction; *i. e.* towards extension of wintering range.

The four species of wader, the subject of this paper, can be grouped, as follows, as to habitat. *T. nebularia*, *T. erythropus* and *T. hypoleucos* favour a small muddy and tidal creek communicating with the main river channel; some visits are made to the main channel. The habitat of *T. ochropus* is very different, being an area of

small pools or an open channel appreciably higher up the river and sometimes above the high tide limit. Vegetation, in some degree, is essential and the habitat is among the »saltings».

1. TRINGA NEBULARIA

Three regular areas are known to me, all being branches of muddy tidal rivers. At high tide the creek is filled and the neighbouring mud-banks are covered with sea-water; during this period the bird, which is usually single, rests on some convenient point on the shore above the tide. I have never observed perching in trees, standing or fallen, during the wintering period by any of these four species.

At low tide a fresh-water stream flows down these creeks.

Arrival and departure on wintering grounds has to be correlated with the known migration period. The general return passage in these areas starts at the end of July; the peak occurs in late August and the movement is dying away about 20th September, although stragglers occur later. The Spring passage does not usually occur until mid April.

By early November the solitary wintering bird has settled: it leaves in mid- or late March.

During January and February the species becomes less cautious and certainly less vocal when disturbed; this is in strong contrast to the behaviour of the ever present *T. totanus*. During winter the upper parts are ash-grey and the underparts almost white; the species is easily seen at a distance.

I have not observed any difference in feeding habits during winter to those used during the breeding season and during migration.

2. TRINGA ERYTHROPUS

I was induced, following the chance discovery of one example of this species in January 1950, to investigate in following years whether such was an accidental occurrence.

I have found that one; and in one year, two; examples have occurred each winter in one of two related areas.

One river is very heavily contaminated with kaolin washed down from china clay mines. Apart from this the habitat is very similar to that described for *T. nebularia*.

A small but regular passage takes place from the end of August till mid October. As yet I am uncertain when the species arrives on the wintering ground but it departs during the first half of March. This may bear some relation to two prior observations by me of single examples in the last half of March at an estuary much further west, where no wintering had taken place and which I assumed to be early passage migrants. Spring passage migrants are very rare in Cornwall.

Wintering examples approximate more to *T. totanus* in their behaviour: they are easily disturbed and the characteristic call-note is frequently heard. In appearance *T. erythropus* in winter dress is much darker than *T. nebularia*.

I have not been able to observe feeding.

3. TRINGA HYPOLEUCOS

Only one area is known to me, but it is not occupied every year. A single bird frequents a tiny gutter, which is a long way from the main channel of the Truro river. In other respects the habitat is very similar to those of the two preceding species.

During January and February the bird is very silent: it flies up readily if disturbed but rarely calls.

4. TRINGA OCHROPUS

It is of particular interest that this species should differ so greatly in its winter habitat from the three preceding species: moreover its winter habitats as observed by me and its resting places on migration in Cornwall are very similar. I have never met with it on an open shore. On passage it is found by gutters, pools and reservoirs, the water being salt, brackish or fresh; but it avoids both the main and secondary river channels to a marked degree, whereas *T. nebularia*, *T. erythropus*, and *T. hypoleucos* frequent all such areas on passage.

Some vegetation is a necessary adjunct to the pools beside which it winters and these are above the normal high tide mark. But I know of one quiet fresh water pond about 100 metres above sea level which is occupied every year.

Often two, and sometimes three, birds can be found in any one area, of which four are known to me.

Return passage begins in early August and lasts throughout September; the sites are occupied in early October, *T. ochropus* being apparently the earliest of the four species to settle for the winter. Departure from these areas takes place about the end of March. A small spring passage takes place in W. Cornwall in mid April.

The species is easily disturbed and remains very vocal throughout the winter. The upper parts appear to be rather lighter but in flight the characteristic black and white contrast remains.

There is a very strong »Ortstreue» exhibited by the first two and the last species. In winter 1947 I found my first *T. nebularia;* the same area has been occupied by one bird every year since and I learned later that it had been independently seen there since 1942. So far I have found that *T. erythropus* is returning to one of two areas each year. In the case of *T. ochropus* one area has been known as a wintering ground for over twenty years.

Only in the cases of *T. nebularia* and *T. erythropus* have I met with some sharing of these winter habitats.

Selbstselektion und Selbstisolation als Weg der intraspezifischen Differenzierung

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Beobachtungen der letzten Jahrzehnte an thermophilen Vogelarten in Westfalen, besser an den Populationen südlicher Arten, die sich hier ihrer nördlichen Ausbreitungsgrenze nähern, sowie an kontinentalen Arten, die hier in das atlantische Klima vorstossen, ergaben, dass diese Populationen überraschend schnell und stark schon auf relativ geringe klimatische Schwankungen durch Bestandszu- oder -abnahme, durch Vorstossen und Zurückweichen reagieren. Dabei war besonders bemerkenswert, dass bestimmte kleinere Gebiete oder Biotope beim Vorstoss zuerst besetzt wurden, selbst weit vor der allgemeinen Ausbreitungslinie, beim Zurückweichen dagegen zuletzt geräumt wurden. So hatte der Rotmilan *(Milvus milvus)* um die Jahrhundertwende in der Münsterschen Tiefebene — einem Pessimum für die Art — besetzte Brutplätze um die 20er Jahre wieder verlassen, die nach der in den 30er Jahren einsetzenden Klimaverbesserung erneut okkupiert, bei der Depression der 50er Jahre wieder aufgegeben wurden. Der Wiedehopf (*Upupa epops* L.) war in der Münsterischen Bucht um die Jahrhundertwende überall Brutvogel, allerdings in unterschiedlicher Dichte. Als die Art bis gegen Ende der 20er Jahre völlig verschwand, hielt sie sich am längsten im Gebiet der Senne, wo sie während der Klimaverbesserung 10 Jahre später wieder und in erheblicher Anzahl sesshaft wurde. Sie siedelte sich dann auch an anderen Orten der Münsterischen Bucht wieder an, verschwand dort aber wieder während der neuen Klimaverschlechterung, während sie sich in der Senne hielt, wo erst jetzt eine Abnahme bemerkbar wird (Peitzmeier 1951, 1958). In diesem Sennegebiet behauptet sich am längsten zu Anfang des vorigen Jahrhunderts auch die Blauracke (*Coracias garrulus* L.) als westfälischer Brutvogel (Landois 1886), hier tauchte sie in der Folgezeit bis jetzt mehrmals — 1899 (Landois 1900), Anfang der 50er Jahre (Moebius 1951, eine unveröffentlichte Beobachtung) — zur Brutzeit wieder auf, wenn es auch anscheinend nicht zur Brut kam. Ähnliche Feststellungen wurden in der Münsterischen Bucht an der Grauammer (*Emberiza calandra* L.) und dem Wendehals (*Jynx torquilla* L). gemacht, für die dieser Raum ebenfalls ein Pessimum darstellt (Peitzmeier a. a. O.). Besonders interessant war das Vorrücken der beiden allgemein sich ausbreitenden Arten, der Wachol-

derdrossel (*Turdus pilaris* L.) und der Türkentaube (*Streptopelia decaocto* Friv.). Der Ausbreitungsvorgang der erstgenannten Art liess einen sehr ausgeprägten Rhythmus zwischen Vorrücken und Auffüllen erkennen. Zuerst schnellten einzelne Paare oder kleine Kolonien über die bisherige Ausbreitungsgrenze vor und liessen sich in offenbar optimalen Biotopen nieder. Dann hörte zunächst das Vorrücken auf und das leere Zwischengebiet wurde aufgefüllt. Man hatte den Eindruck, dass der Vorstoss nur widerwillig geschieht und Anschluss an den Ausgangsraum gesucht wird. Trotzdem wurden aber immer wieder isolierte vor der Ausbreitungsfront liegende, offenbar besonders geeignete Biotope zuerst besetzt (PEITZMEIER 1953). Im Ausbreitungsgeschehen der Türkentaube wurden in Westfalen alle Trockengebiete, einige geschützte Lagen oder Kleinbiotope im Sauerland und der Südrand des Teutoburger Waldes besiedelt. Aus der Münsterischen Bucht dagegen ist bis heute noch kein Brutvorkommen ermittelt, sie wird aber von Brutplätzen geradezu eingerahmt (PEITZMEIER 1957).

Alle diese Beobachtungen sind schöne Beispiele dafür, dass die Vögel bei ihrer Ausbreitung ein sehr feines Empfinden für günstige Biotope haben, diese »planmässig» suchen und sich im optimalen Biotop so lange wie möglich behaupten.

Diese Biotopwahl muss m. E. auch eine Rolle gespielt haben in der rassischen Differenzierung. Die Tatsache, dass Rassen sehr oft klimatisch verschiedene geographische Räume bewohnen, dass man darauf die BERGMANNsche Regel, der physiologische Bedeutung zuerkannt wird, aufbauen konnte, in Verbindung mit der in zahlreichen Experimenten an vielen Tierarten nachgewiesenen erblichen Veranlagung für die Bevorzugung bestimmter Temperaturen, lässt den Schluss zu, dass die Biotopwahl ein Faktor in der Rassenbildung sein kann.

Voraussetzung für jede rassische Differenzierung sind Selektion und Isolation. In den gebräuchlichen Handbüchern fasst man diese ausschliesslich als mechanische Wirkungen der Umwelt auf: Eine Population wird durch äussere Faktoren, etwa Verdriftung, von anderen räumlich getrennt. Durch die im neuen, ihr mechanisch zugewiesenen Lebensraum wirksamen Selektionsbedingungen werden bestimmte, zufällig vorhandene Mutanten gefördert und ausgelesen, sodass im Laufe der Zeit diese Population sich von der ursprünglichen genetisch unterscheidet. Dass dieser Weg oft zur Rassenbildung geführt hat, steht ausser Zweifel. Daneben kann aber auch, vor allem bei Vögeln eine vom Organismus gesteuerte Selektion und Isolation eine Rolle gespielt haben.

Wenn wir annehmen können, dass manche Vogelrassen sich in ihrer Temperaturtoleranz von anderen erblich unterscheiden, — hierüber sind experimentelle Untersuchungen sehr erwünscht, — dann muss diese Eigenschaft mutativ entstanden sein. Solche, die ökologische Valenz der Art erweiternde Mutationen können sich innerhalb der Population vermehren und lange Zeiten hindurch latent bleiben. Wenn aber infolge günstiger Verhältnisse eine Übervermehrung stattfindet und zur Arealausweitung drängt, dann können diese Mutanten als Pioniere weit in neue klimatisch andere Räume vorrücken, wohin ihnen die übrigen Angehörigen der Population

nicht folgen. Infolge des sehr feinen Empfindens für optimale Biotope finden die Mutanten ganz bestimmte zusagende Lebensräume, wo sie sich treffen, sammeln, und infolge des Nischeneffekts schnell vermehren können. So haben sie sich selbst ausgelesen und von der Ausgangspopulation isoliert. Im neuokkupierten Areal kann dann unter neuen Selektionsbedingungen *sekundär* auch eine morphologische Differenzierung erfolgen. Der Weg zur Rassenbildung wäre in solchen Fällen also der folgende: 1) Entstehung ökologisch relevanter Mutationen, 2) die psychologische Reaktion darauf im Sinne der Biotopwahl, 3) dadurch bewirkte Selektion und Isolation, 4) weitere, auch morphologische Differenzierung im isolierten Raum infolge neuer Auslesebedingungen. Es will scheinen, dass die feinen Abstufungen horizontal verbreiteter Rassen im Sinne der Bergmannschen Regel, die Existenz ökologischer Rassen auf engstem Raum und von Vertikalrassen, u. U. am gleichen Bergmassiv, am besten durch Selbstselektion und Selbstisolation verständlich gemacht werden können. Es braucht nicht besonders hervorgehoben werden, dass neben Mutationen der klimatischen Toleranz auch andere Mutationen ökologischer Natur sich in der gleichen Weise durchsetzen können.

Selbstselektion und Selbstisolation können den Rassenbildungsprozess erheblich beschleunigen, zumal die Ausgangspopulationen verhältnismässig klein sind.

Ernst Mayr (1926) war wohl der erste, der in seiner Girlitzarbeit auf die Möglichkeit hinwies, dass bei starker Arealausweitung vor allem südlicher Arten nach Norden ökologische Mutanten wirksam sein könnten. Später wurde in vielen Arbeiten die Bedeutung der Biotopwahl erwähnt. Es war der Zweck dieser Ausführungen, an Hand von Beispielen aus der deutschen Vogelwelt auf die in der allgemeinen Diskussion des Entwicklungsgeschehens bisher wohl zu sehr vernachlässigte Biotopwahl besonders hinzuweisen.

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Les routes de migration de quelques oiseaux d'Europe et l'opportunité de coordonner l'oeuvre des nombreuses Stations de Baguage

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En Europe, le baguage, depuis quarante ans environ, se développe activement presque partout.

Au cours de ces dernières années il y a eu un essort très remarquable. En Finlande, parti de 4,000/5,000 oiseaux par an, on est arrivé en 1955 à 25,000 oiseaux. Le même chiffre fut obtenu en Suisse. La Finlande en 1955 a opéré sur 149 espèces, et par conséquent l'étude est étendue à une grande partie de l'avifaune.

Comparativement à cet immense travail on remarque, par contre que l'étude des résultats est assez limitée. Cette étude serait très opportune car on pourrait àrriver à la divulgation des notions acquises. On a récemment constitué lors du Congrès ornithologique international, un Comité de coordination de l'oeuvre du baguage. Nous souhaitons qu'il atteigne les buts pour les quels il a été constitué et qu'il puisse bientôt faire connaître son activité.

J'ai voulu examiner, quoique d'une façon très succinte (et je suppose incomplète) les rapports de trois importantes Stations de baguage: Helsinki, Bruxelles, Sempach, et je vais résumer ce que j'en ai tiré.

J'ai aussi pris en considération les notices publiées dans les comptes-rendus des dites Stations et concernant les reprises effectuées en Belgique, Finlande, et Suisse, d'oiseaux bagués par des Stations étrangères.

Par mon travail j'entends rendre honmage au précieux travail, accompli dans ces stations par Monsieur Dr. I. Välikangas et G. Nordström de Helsinki; Ch. Dupond de Bruxelles et A. Schifferli de Sempach.

Motacilla alba L. Les individus bagués en Belgique descendent vers la France du Sud, en traversant, en pleine période de passage automnal, la région de la Gironde pour se rendre ensuite ne Espagne, au Portugal et au Maroc. Le comportement migratoire est très voisin de celui de *Budytes flavus* par rapport a la route de migration; mais tandis que cette dernière espèce ne s'arrête pas pour hiverner, en Europe continentale, au contraire un grand nombre de *Motacilla alba* hivernent sur le continent. Pour cette espèce on n'a pas remarqué la vitesse de déplacement de la *B. flavus*.

Les finnois tout en ayant travaillé sur une remarquable quantité d'individus, n'ont enrégistré que très peu de reprises.

Toutefois elles nous ont revélé une direction S.S.E. qui devra être pourtant confirmée par le travail des années à venir.

Je cite un individu, bagué près de Helsinki le 14. 6. 33, repris à Jaffa (Palestine) le 13. 11. 33, Km. 3,250 S.S.E.; le no. 20166 bagué à Helsinki le 12. 7. 34 repris à El ZarKa (Egypte) le 29.5.35, Km. 3,400 S.S.E (il faut remarquer que cet individu s'est très probablement maintenu en Egypte pendant l'été 1935); et encore le no. 47853 bagué à Rauma le 11. 7. 1939 repris à Rosetta (Egypte) le 10. 1. 40, Km. 3,400 S.S.E.

Parmi les sujets bagués en Suisse nous signalons deux captures en Espagne (S.W.) et une capture près de Salerno (Italie) a S. pendant l'hiver qui a suivi le baguage.

Budytes flavus (L.) Pour cette espèce je prends en considération seulement les résultats de la Station de Bruxelles qui sont toutefois très instructifs. On connaît bien une route de migration de la Belgique à la région des Landes (France) où les migrateurs arrivent en pleine période de passage, en toute probabilité transitant vers la péninsule ibérique et l'Afrique. Il y a eu des captures au Portugal et au Maroc.

Pour la remarquable vitesse de déplacement je cite le no. 6A6175 bagué à Rhode St. Genèse le 7. 9. 34 repris le 14 et le 20. 9. 34 à Milagres (près de Leiria, Portugal) Km. 1,655 S.O.

Si l'on considère exacte la date de la première capture il en résulte une vitesse moyenne de 236 Km. par jour (c'est peut être la plus grande vitesse connue pour les petites espèces).

La rapidité de cette espèce lors de ses voyages d'automne nous a été confirmée par d'autres reprises, signalées dans la région des Landes (France), et qui donnent, après des vols de presque 1,000 Km., des vitesses de 83—90 Km. par jour.

Un autre trait caractéristique de cette espèce est sa tendance à suivre en automne, pendant des années consécutives la même route de migration: en effet on a fait en Belgique plusieurs captures au mois d'août-septembre, dans la même région de baguage et à une année de distance.

Anthus pratensis (L.) — Seule la Belgique nous donne quelques reinsegnements; en effet la quantité baguée par Helsinki et Sempach est trop faible. On a capturé plusieurs oiseaux belges dans la région de la Gironde et dans la France du Sud: on a eu d'autres reprises en octobre, novembre, janvier, en Espagne et Portugal: je cite le no. 5 A. 2901 bagué à Borgloon il 4.10.54 repris dans la prov. de Cadix le 4. 11. 54, (Km. 1,825 S.O. (Km. 60 par jour.)

Une vitesse de 73 Km. par jour a été contrôlée par une capture effectuée en France (Lat-et-Garonne) après un vol de 800 Km.

Nous jugeons intéressant d'intensifier le travail sur cette espèce surtout dans l'Europe du Nord.

Anthus trivialis (L.) — Les résultats de la Station belge nous disent qu'une bonne partie des individus bagués en Belgique, pendant le passage d'automne, se dirigent vers l'Espagne et le Portugal où ils ont été repris un ou deux mois après le baguage et mêm à fin décembre et en mars. On remarque une capture au Maroc, sans date.

Le baguage finnois a démontré une tendance des migrateurs à se diriger vers l'Italie où l'on a effectué des captures aux mois d'août et septembre à S. Daniele del Friuli, Vicenza et Pistoia deux ou trois mois après le baguage (distance Km. 2,000—2,200).

Muscicapa striata (Pall.) — Les résultats des baguages belges et suisses ont mis en évidence que les individus de cette espèce se dirigent vers l'Espagne, le Portugal puis vers l'Afrique où ils ont été retrouvés au Congo Belge et en Nigeria. Je cite le no. 5A5058, bagué au nid à Lauden (Belgique) le 21. 6. 33 repris le 16. 8. 33 près de Valpassos (Portugal) Km. 1,400 S.O., probablement migrant vers l'Afrique; le no. E. 20332 Praha bagué près de Hluboké (Tchéco-Slovaquie) repris à Thysville (Congue Belge) le 3. 11. 39 après un an, 3 mois et 10 jours; un individu jeune, bagué à Arbon le 15. 6. 33 repris à Ezira le 17. 10. 33 Km. 4,500. Les sujets bagués en Finlande ont généralement suivi une route Nord- Sud. ainsi que le no. 63756 bagué à Helsinki le 1. 7. 52 repris

à Chalcis (Grèce) le 10. 10. 52 Km. 2,460 S., le no. 68937 bagué à Korsholm (63°11′ N. 21°40′ E) l'8. 7. 54 repris près de Ferndale (Johannesbourg 26°5′ S. 28 E.) le 15. 1. 55, Km. 10,020 S. (environ 56 Km. par jour, toujours en admettant que le sujet venait d'arriver au moment de la capture); un autre sujet bagué en Finlande en juillet 1955 fut repris en Afrique du Sud (Kapland) en février 1956 — Km. 10,560 S. On remarque aussi une reprise au Portugal d'un sujet finnois. En Finlande on a enregistré quelques reprises en juin d'individus bagués l'année précédente au même lieu.

Muscicapa hypoleuca (Pall.) — Le travail finnois nous a donné de bons résultats et nous a montré d'une façon très claire la migration de cette espèce vers la péninsule ibérique; de nombreuses captures eurent lieu au Portugal de la fin d'août jusqu'en octobre. Cette route de migration passerait par la région de la Gironde (dans la France du Sud). Parmi les captures connues, je cite la suivante, remarquable pour la vitesse de déplacement; le no. 83322 bagué à Hämeenkyrö le 1. 7. 54 repris à Macedo de Cavaleiros (Portugal) le 29. 8. 54 Km. 3,090 S.O. (Km. 52 par jour); nous remarquons la migration précoce de cet individu. La Station de Sempach a enregistré plusieures reprises au même lieu de baguage à une année de distance.

Rien à signaler de la Station de Bruxelles qui (comme a remarqué D. DUPONT lui même) devrait apporter plus d'attention à cette espèce.

Phoenicurus phoenicurus (L.) — Les résultats des deux Stations de Bruxelles et de Sempach nous disent que cette espèce migre vers la péninsule ibérique et l'Afrique tandis que les résultats de Helsinki signalent même une capture en Roumanie; le no. 1412 bagué à Signilskär (Åland) le 22. 9. 33, repris en station d'hiver à Orhei (Bessarabie-Roumanie) le 23. 11. 33 Km. 1,575 S.S.E; il y a eut une autre reprise en Italie, ce qui prouve que les sujets provenant de Finlande, ne se dirigent pas seulement vers la péninsule ibérique mais suivent aussi des routes de migrations Nord-Sud et Nord-Sud-Est, dans leurs voyages vers les quartiers d'hiver.

Les résultats des trois Stations sont d'accord sur la tendance de *Phoenicurus phoenicurus* à retourner aux mêmes lieux où ils ont nidifié, où ils sont nés et ont été bagués les années précédentes.

En Suisse on les a retrouvé à une année de distance, dans les mêmes jardins.

Phoenicurus ochruros gibraltariensis (Gmelin) — Cette espèce, partiellement sédentaire, migre aussi vers la peninsule ibérique et l'Afrique, comme il résulte des résultats du baguage des Stations de Sempach et de Bruxelles. Je cite le no. 1 A. 3749 bagué sur nid près de Limburg (Belgique) le 5. 6. 50 et repris près de Cordobe (Espague) le 4. 1. 51 (Km. 1,625 S.O.) et un individu jeune bagué à Henggart (Suisse) le 14. 6. 35 repris à Malaga le 1. 12. 35 (Km. 1,580 S.O.).

Erithacus rubecula (L.) — Cette espèce, sédentaire en bonne partie en Belgique et en Suisse, comporte un contingent remarquable, soit baguée au nid, soit baguée en migration d'automne, qui migre régulièrement, vers l'Espagne, le Portugal, et l'Afrique du Nord (Algérie) où les individus ont été retrouvés l'automne ou l'hiver suivant le baguage.

Je cite le no. 284932, bagué adulte à Lausanne (Suisse) le 21. 11. 50 repris près de Constantine (Algérie) le 5. 2. 51, pour la migration tardive et le no. 6A4437 bagué a Crainhem (Belgique) le 29. 9. 34 repris près de Albufeira (Portugal) le 11. 5. 35 Km. 1,865 S.O, ce qui fait supposer que le sujet est demeuré au Portugal pendant l'été 1935.

De Finlande nous connaisons peu de captures effectuées fin octobre et dans la première décade de novembre dans les Basses Pyrénées et dans la région du Var (France).

L'une de ces reprises a donné une vitesse de migration de 79 Km. par jour sur une distance de Km. 2,360. En Belgique on a capturé pendant la période de passage automnal, et en quartier d'hivernage, des individus provenant de la Suède.

Sylvia borin (Bodd.) — Les résultats les plus intéressants sont ceux de la Station d'Helsinki. D'après lesquels on sait que les sujets bagués dans ces régions se dirigent vers l'Italie ou ils ont été retrouvés dans les premiers jours de septembre, deux mois environ après le baguage.

On peut pourtant supposer que normalement *Sylvia borin* parcourt les 2,000 Km. environ

qui séparent la Finlandie de l'Italie en deux mois. Le no. 67961 a constitué une exception. Bagué dans l'Ile d'Åland le 25. 8. 54 a été repris à Piombino (Livorno) Italie — le 19. 9. 54 — Km. 2,050 S.S.O. (Km. 82 par jour).

On connaît une capture, effectuée fin septembre au Portugal, d'un individu bagué en Juin en Belgique et une capture en hiver en Espagne d'un sujet bagué en Suisse.

Hippolais icterina (Vieill.) — Les résultats des baguages des Stations de Bruxelles et de Sempach ont mis en évidence que cette espèce migre vers le S.Est. On connaît des reprises effectuées à Lovere (Bergamo, Italia), près de Rome et à Salerne. Pour la vitesse de déplacement je fais remarquer le no. 16 A 2466 bagué à Merxem (Anvers) le 6. 8. 47, repris à Frosinone (Italie) le 26. 8. 47 — Km. 1,280 S.E. (Km. 64 par jour); nous remarquons enfin qu'en Belgique, en juillet 1952 on a capturé un individu (no. 19 A 328) dans la même place où il avait éte bagué au nid en juin 1949.

Aucun résultat de la Station d'Helsinki.

Acrocephalus scirpaceus (Hermann) — L'oeuvre Suisse nous a fait connaître des reprises en Espagne, et de plus une reprise particulièrement intéressante d'un individu bagué le 28. 8. 40 à Sempach (Suisse) retrouvé le 2. 2. 41 dans le Togo (Afrique) Km. 5,300 S.S.O. En Suisse on a eu plusieurs reprises en mai, juin et juillet dans les lieux mêmes où les individus ont été bagués l'année précédente. En Belgique aussi il y a eu un cas analogue.

Phylloscopus trochilus (L.) — La Belgique et la Finlande ont enregistré quelques reprises en été dans le lieu même du baguage un ou deux ans avant.

En ce qui concerne la migration, la Station de Sempach signale quelques reprises en Espagne et Portugal. Pour la migration exceptionellement précoce je signale le no. 308465 bagué à Chessel (Suisse) le 29. 5. 55 repris à Senide (Coimbra-Portugal) le 18. 8. 55. Km. 1,400 S.O.

Lanius collurio L. — Le baguage suisse ainsi que le baguage belge indiquent que les individus de cette espèce migrent en direction S.E. Je cite comme exemple un individu bagué jeune à Realpe (Suisse) le 24. 9. 35 repris à Beyrout en avril 1936 (Km. 2,680 S.E.), le no. 301644 bagué au nid le 27. 6. 51 à S. Sulpice, repris à l'Ile Syros (Archipel grec) le 10. 9. 51, Km. 1,850 S.E.; le no. 65563 avec bague Viborg-Danemark — bagué au nid aux îles Taasinge (Danemark) le 5. 7. 41, repris à Yangalla (Congo Belge) en juin 1942 Km. 5,100 S.S.E.; il est intéressant de remarquer que ce dernier individu n'a pas migré vers l'Europe pendant l'été 1942. Un autre individu bagué en Belgique en juin a été repris en Hongrie en septembre — Km. 1,100 E.S.E. — Le travail de la Station de Bruxelles a mis en évidence une tendance marquée du *Lanius collurio* à retourner l'été dans les régions où il est né et où il a nidifié.

Aucun résultat pour la Finlande, faute d'un nombre suffisant de reprises.

Carduelis carduelis (L.) — Il s'agit dans la plupart des cas d'une espèce sédentaire; toutefois quelques sujets bagués en Belgique et en Suisse sont arrivées jusqu'en Espagne.

Pendant le passage automnal, des individus provenant de l'Allemagne du Nord (Station de Helgoland) transitent par la Belgique. La vitesse de déplacement de cette espèce est assez grande. Par exemple le no. 8068—613 Helgoland, bagué le 2. 10. 34 à Solingen (Renanie, Allemagne) a été repris le jour suivant à Welkenraedt (Belgique) Km. 100 S.W. D'autres résultats ont indiqué des vitesses analogues. Il faut encore citer la capture effectuée en Belgique près de Saint Vith du no. 859014 Helgoland, bagué près de Dessau (Allemagne) 16 ans et 8 mois auparavant.

Il nous paraît opportun d'intensifier le baguage de *Carduelis carduelis* surtout dans les régions du Nord de l'Europe.

Carduelis spinus (L.) — Nous devons nous baser seulement sur les résultats de la Station belge car l'oeuvre finnoise et suisse ne porte que sur quelques dizaines d'individus par an environ. Nous souhaitons que ces deux importantes Stations puissent à l'avenir porter leurs soins sur *Carduelis spinus* ce qui donnerait des résultats intéressants surtout en ce qui concerne la vitesse de déplacement pendant la migration. Les individus de passage en Belgique en automne proviennent de Scandinavie, d'Allemagne et de Hollande.

Je signale comme très instructif au sujet de la vitesse de migration de cette espèce le no. 397313 Rossitten bagué à Berlin le 11. 11. 36 repris le 14. 11. 36 près du Gand (Belgique) Km. 670 N.O. (190 Km. par jour) et le n. F. 47622 Leiden bagué près de la Hage (Pays-Bass) le 10. 10. 48 repris à Merxplas (près de Anverse-Belgique) le 11. 10. 48 (Km. 120 par jour). Un autre individu bagué en Belgique en octobre 1929 a percouru 130 Km. en un jour.

Les résultats de l'oeuvre belge sur le déplacement vers le sud du *Carduelis spinus* sont très limités.

Je citerai par contre une reprise effectuée en Angleterre pendant la troisième décade de novembre, d'un individu bagué environ un mois avant dans le Hertogenwald (Km. 500 N.O.).

Carduelis cannabina (L.) — Les individus qui traversent la Belgique pendant le passage d'automne proviennent, d'après les indications des baguages, spécialement de la Hollande et du Danemark.

Le baguage belge a prouvé l'existence d'une route de migration importante qui, de la Belgique, arrive à la région de la Gironde en France et de là en Espagne, pour un contingent que nous considérons limité et pour lequel il y a eu quelques reprises (Valencia, Cadise, La Ronda).

On remarque une reprise en Angleterre au mois de décembre.

Comme vitesse de migration, nous avons eu, toujours d'après les résultats de la Station de Bruxelles, des indications donnant 80 Km. par jour, environ. Parmi les résultats de la Station suisse, nous n'avons à signaler que peu de reprises enregistrées en Espagne. Le matériel bagué en Finlande est trop limité pour nous fournir des indications.

Fringilla coelebs L. — L'intérêt du baguage suisse, effectué en hiver et en été, est très limité, car les individus bagués au cours de ces deux saisons sont résultés sédentaires. Le baguage pendant le passage automnal pourrait au contraire donner des résultats intéressants. Pendant le passage automnal on a capturé en Belgique des individus bagués en Norvège (Moss) Suède (Stockholm) Finlande (Janakkala) et Allemagne (Heligoland).

Les individus bagués en Belgique pendant le passage automnal ont aussi donné des résultats intéressants: plusieurs individus ont été repris en Grande-Bretagne et nous pouvons sans aucun doute affirmer que pour cette espèce il y a un remarquable courant migratoire Belgique — Grande-Bretagne — également prouvé par des reprises effectuées en Belgique en automne, d'individus marqués en hiver en Angleterre. Des reprises significatives ont été effectuées en Espagne et en Portugal. Je cite le no. 11 B 7063 bagué à Nison lez Verviers le 6. 10. 47 repris à Fafe (Portugal) le 8. 12. 47 — Km. 1,400 S.O. le no. 14 A 9661 bagué près de Liège le 22. 10. 55 repris a Irun (Espagne) le 13. 11. 55 Km. 1,000 S.O. et le no. 5 B 9821 bagué à Haversin le 15. 10. 33 repris dans les environs de Jemein (Vircaya) Espagne le 30. 10. 33 Km. 1,000 S.O. (66 Km. par jour).

Quelques reprises ont été signalées en France dans les Landes; et parmi celles-ci il y en a une très importante: le no. 16 B 503 bagué a Aische-en — Refail (Namur) le 14. 10. 47 repris à Solferino (Landes-France) le 18. 10. 47 Km. 825 S.O. (Km. 165 par jour).

Les reprises suivantes sont aussi intéressantes: le no. 8 A 1711 bagué à Jupille le 1. 11. 32 repris vers le 15. 5. 33 à Jarensh (N.E. de la Russie) Km. 2,930; le no. 10 B 254 bagué près de Namur le 20. 10. 37 repris à Leningrad le 10. 6. 39 Km. 1,875 N.E. et un; individu bagué jeune, en Hollande le 16. 10. 49, repris à Leningrad le 28. 5. 52 Km. 1,900 N.E.

Fringilla montifringilla L. — D'un certain intérêt sont les suivants résultats de la Station de Sempach: individu bagué le 29. 1. 39 à Luzern (Suisse) repris le 16. 1. 40 près de Prizzen (Iugoslavie) Km. 1,100 S.E. et un autre individu nagué encore à Luzern le 5. 2. 39 repris le 18. 3. 40 à Gradistea (Romanie) Km. 1,200 E.S.E.; ces deux reprises font supposer que la région de provenance de cette espèce se trouve beaucoup plus à l'Est que la Suisse; les deux individus qui avaient hiverné en Suisse en 1939 l'année suivante, en effet ont avancé plus au Sud tout en restant vers l'Est.

Les individus qui arrivent en Belgique, pendant l'automne, proviennent surtout du Nord

de l'Allemagne, quoique il ne manque pas de captures d'individus bagués en Scandinavie. Le baguage finnois nous a fait connaître une capture très intéressante concernant le no. 56601 bagué dans l'ile de Åland le 14. 4. 51 et repris dans la province de Tolède (Espagne) le 1. 3. 53, Km. 2,750 S.O. L'examen des comptes-rendus des trois Stations pour une période de trente ans environ, me permet de faire quelques considérations que je crois bon faire connaître.

TENDANCE DE QUELQUES ESPÈCES A RETOURNER À LEUR LIEU D'ORIGINE OU DE NIDIFICATION

Il faut ajouter aux espèces déjà citées à ce propos: *Budytes flavus, Lanius collurio, Muscicapa hypoleuca, Muscicapa striata, Phylloscopus trochilus, Phoenicurus phoenicurus* les espèces suivantes: *Cuculus canorus, Parus major, Sylvia communis, Oenanthe oenanthe, Saxicola torquata rubicola, Luscinia megarhyncha.*

Vitesse de migration: Il faut ajouter aux vitesses signalées pour les espèces particulièrement prises en considération: *Sturnus vulgaris;* (sujet bagué le 2. 10. 39 à Sempach (Suisse) repris le 9. 10. 39 en Algérie Km. 1,200 (Km. 170 par jour); le No.F. 155—824 Rossitten bagué le 18. 19. 10—1933 au Phare de Grand Horst (Pomeranie) repris le 23. 10. 33 à Knocke sur Mer (Km. 845 (169 Km. par jour); le No. 760280 Zoo Museum Danemark bagué le 20. 10. 39 à l'Ile de Christianso (Danemark) repris trois jours après, près de Gand (Belgique) Km. 635—210 km. par jour.

Anas querquedula: le No. 3 E 3197 bagué àdulte à Metkerke (Belgique) le 29. 3. 55, repris près de Kotchenevo (Sibérie) le 15. 4. 55, Km. 4,750 E.NE. — Km. 279 par jour.

Longévité: J'ajoute aux cas déjà signalés: pour *Sturnus vulgaris:* le No. 4 C 1750 bagué à Knokke-au-Zee (Belgique) le 15. 11. 35 repris le 3. 12. 55 dans le même lieu après avoir gardé la bague pendant vingt ans; pour *Falco peregrinus* le N. 757 bagué le 14. 7. 18 à Kirchspiel Karvia (Finlande) repris le 8. 10. 33 en Kirchspiel Haapavesi à 265 Km. de distance, après 15 ans; pour *Accipiter nisus* le N.A 1593 Stockholm bague le 15. 6. 27 près de Lukkasjärvi (Laponie) (Suède) repris le 22. 5. 42 près de Liège Km. 8,800 S.SO. après presque 15 ans.

Le travail que les différentes Stations accompliront à l'avenir prouvera si la tendance à retourner dans les pays d'origine et de nidification est pour quelques espèces vraiment habituelle ou accidentelle et surtout nous fournira des notions plus complètes sur la vitesse et la longévité des espèces mentionnées.

The Effects of Climate and Weather on the Birds of the Falkland Islands

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The Falkland Islands rise from the South Atlantic about 800 miles north of Antarctica's Palmer Peninsula and 300 miles east of South America's southernmost extremity. Although well over 100 islands and islets comprise the archipelago, a major portion of its 4,618 square miles of land surface is shared almost equally by two main islands, East Falkland and West Falkland. Excluding Beauchene Island that lies 50 miles south of the archipelago, all the islands are confined to a space 130 miles (east-west) by 80 miles (north-south) between latitudes 52° and 53° South, and longitudes 57° and 62° West. The lands nearest the Falklands, after South America, are the South Shetland Island 600 miles directly south, and the South Orkney Islands, 700 miles southeast.

CLIMATE AND WEATHER

In any season the climate of the Falklands is cool. Never does one sense complete, satisfying warmth. Even on the pleasantest summer day there is a lurking chill—the kind we know in the Northern Hemisphere when spring is still in winter's grip. On the other hand never does one suffer prolonged, freezing cold. From season to season the air temperature changes imperceptibly with the result that the thermal range between summer and winter is scarcely more marked than it is on islands in the Caribbean and Mediterranean Seas.

The mean annual temperature is 43° F. with an annual range of only 12° between the coldest month (July, 37° F.) and the warmest month (January, 49° F.). In London, which is as far north of the Equator as the Falklands are south, the annual temperature is 50° F. with a range of 24° — twice as great — between the warmest and coldest months (July, 63° F., and January, 39° F.). Thus the Falklands are cooler in the summer and slightly colder in the winter.

The Falklands owe their steady, year-round coolness to the influence of the ocean itself and to its circulation in particular. Without discussing here the geophysical

basis for ocean currents, let it suffice to say that the general direction of flow in the southern oceans of the world is circumpolar, from west to east. But in the neighborhood of South America this flow is temporarily deflected by the long Patagonian peninsula to a circuitous course through Drake Strait, south of Cape Horn. In its southward passage its waters inevitably converge with icy waters from the Antarctic, with the result that its temperature is considerably lowered. On reaching the Atlantic, the flow — now very cold — fans out and divides: the smaller part, or Falkland Current, sweeps northward, past both sides of the Falklands; the larger or the main part moves northeastward, toward South Georgia.

The effect in the Falklands of the continuous passing of the cold, deep Falkland Current is to keep the air cool at all times. To the west the effect of the Falkland Current becomes less pronounced for its waters soon mix with the warmer, shallower waters near South America and lose much of their cooling quality. As a consequence, the air on the coast of Patagonia at the same latitude as the Falklands averages 13° warmer.

Probably no part of the world permanently settled by man has a more disagreeable climate than the Falklands. This is due largely to their position in the high latitudes of the Southern Hemisphere where the winds blow with almost incessant fury, causing a general unsteadiness of weather. Rarely do sky conditions remain the same for as long as a half day. The fact that one may be enjoying bright sunshine in the morning is no assurance whatever that by afternoon he will not be battling a severe storm.

The winds that lash the Falklands are the great »westerlies». Their prevailing direction is actually from the northwest, but they also come frequently from the west and southwest and even from the north. Winds from any other direction are unusual. Still more unusual is a calm, when there is no wind at all. Normally, in the course of twenty-four hours, the wind shifts from a northerly direction at night to a westerly direction in the afternoon, and then back again. There appears to be no marked correlation between wind direction and season. Summer or winter the direction is usually the same, although during the winter the percentage of south winds increases slightly, but never enough to have an appreciable effect on the average daily temperature.

It is their strength, as much as their persistance and westerly direction, that makes the winds an important environmental factor. Throughout the year their average velocity is 17 to 18 miles an hour. For more than two-thirds of the time the speed is between 13 and 38 miles an hour, while gales (39 to 54 miles an hour) occur three percent of the time. Usually the winds are unsteady, coming in forceful gusts with intervening, irregular periods of diminished velocities. Although the spring and fall months tend to be windier, gales take place in any month. At night the winds moderate to some extent but have the same unsteady character.

Rainfall in the Falklands averages 26 inches a year, just slightly more than London's average of 24. But the mean number of days with rain or showers is far greater,

being 240 to London's 167. Though the summer months are the wettest, there is no month without a considerable share of the precipitation. Hail and sleet each occur at least two or three times a month; and snow falls one or more times in all months, except January and February, but seldom stays long on the ground.

The year-round climate is consistently damp, with a daily mean relative humidity of 84 percent. Expectedly, there is considerable cloudiness, but on the average there are only 60 days a year that are completely overcast from beginning to end. On all other days there are at least brief intervals of sunshine. Totally cloudless days are, however, very rare. In some years there may be one to several, in others, none.

BIRD LIFE

Birds are the dominant animals in the Falklands. There are no reptiles and amphibians. Four species of seals and a fox, presumably extinct, are the only native mammals. In ponds and streams live two species of small fish. Insects and non-marine invertebrates are remarkably sparse — a fact that I shall elaborate upon later in this paper.

The fifty-one species of birds known to breed regularly in the Falklands are listed below. Two species, Rolland's Grebe and Falkland Flightless Steamer Duck, are considered endemic, while the populations of 12 other species (each marked by an asterisk) are declared by one or more authorities to be racially distinct from populations of the same species in South America.

Gentoo Penguin, *Pygoscelis papua*
Rockhopper Penguin, *Eudyptes crestatus*
Jackass Penguin, *Spheniscus magellanicus*

Rolland's Grebe, *Podiceps rolland*
Crested Grebe, *Podiceps occipitalis*

Black-browed Albatross, *Diomedea melanophris*
Giant Fulmar, *Macronectes giganteus*
Slender-billed Whalebird, *Pachyptila belcheri*
Shoemaker, *Procellaria aequinoctialis*
Sooty Shearwater, *Puffinus griseus*
Wilson's Petrel, *Oceanites oceanicus*
Gray-backed Petrel, *Garrodia nereis*
Diving Petrel, *Pelecanoides urinatrix*

Rock Shag, *Phalacrocorax magellanicus*
King Shag, *Phalacrocorax albiventer*

*Black-crowned Night Heron, *Nycticorax nycticorax*
Black-necked Swan, *Cygnus melanocoryphus*
*Kelp Goose, *Chloëphaga hybrida*
Upland Goose, *Chloëphaga picta*
Ruddy-headed Goose, *Chloëphaga rubidiceps*
Crested Duck, *Lophonetta specularioides*
Falkland Flightless Steamer Duck, *Tachyeres brachypterus*
Flying Steamer Duck, *Tachyeres patachonicus*
Yellow-billed Teal, *Anas flavirostris*
Chiloë Widgeon, *Anas sibilatrix*
Silver Teal, *Anas versicolor*
Turkey Vulture, *Cathartes aura*
Red-backed Hawk, *Buteo polyosoma*
Forster's Caracara, *Phalcobaenus australis*
Southern Caracara, *Polyborus plancus*
Peregrine Falcon, *Falco peregrinus*

Fuegian Oystercatcher, *Haematopus leucopodus*
Black Oystercatcher, *Haematopus ater*
Falkland Plover, *Charadrius falklandicus*
Winter Plover, *Zonibyx modestus*
Paraguayan Snipe, *Capella paraguaiae*
Skua, *Catharacta skua*
Dolphin Gull, *Leucophaeus scoresbii*
Kelp Gull, *Larus dominicanus*

Brown-headed Gull, *Larus maculipennis*
Cassin's Tern, *Sterna hirundinacea*

*Short-eared Owl, *Asio flammeus*

*Tussockbird, *Cinclodes antarcticus*
*Garnot's Ground-tyrant, *Muscisaxicola macloviana*
*Short-billed Marsh Wren, *Cistothorus platensis*
*Neotropical House Wren, *Troglodytes musculus*
*Falkland Robin, *Turdus falcklandii*
*Correndera Pipit, *Anthus correndera*
*Red-breasted Troupial, *Pezites militaris*
*Black-chinned Siskin, *Spinus barbatus*
*Black-throated Finch, *Melanodera melanodera*

EFFECTS OF CLIMATE AND WEATHER

On the Length of the Breeding Season. With an average difference of only a few degrees between summer and winter, local conditions for breeding are suitable at any time of the year. The sea, harbors, streams, and ponds remain ice-free; no snow covers the ground at low elevations for any appreciable time. Except for insects, which may be reduced during the winter by frosts and occasional below-freezing temperatures, food is always available. Winter is scarcely recognizable from spring, and spring from summer. Thus, unlike the changing seasons in many other parts of the world's temperate zones, there is no abruptness about the coming of spring, no sudden rush of new life.

As a result of this remarkably equable, year-round climate, most bird species have a long breeding season. At least three ducks — the Flightless Steamer Duck, Crested Duck, and Yellow-billed Teal — nest through nearly all the year, laying in August (rarely in July) and being with broods as late as April and even May. The Upland Goose, Turkey Vulture, Red-backed Hawk, and most of the shore birds begin nesting in September; and the Falkland Robin nests from September through January, during which time it undoubtedly rears two or more broods.

Despite the peculiarities of the Falkland climate, the breeding season of sea birds — penguins, procellariiform birds, shags, gulls, and terns — is no longer than in other parts of the world. The Black-browed Albatrosses nest earliest, in the first of October, and the gulls and terns latest, in mid-December. The first young to leave their nests are those of the King Shags, in late February; the latest are those of the procellariiform birds. All hold to an inherent pattern that dictates one nesting a year at specific time, regardless of climate.

It is noteworthy that the Skuas and gulls nest much later than the penguins and shags on whose colonies they depend heavily for food, such as eggs, downy young, and the inevitable accumulation of dead young killed by various factors at different stages of growth. In all probability this late nesting is an adaptation that assures the Skuas and gulls of an increased food supply when they begin nesting and, later, when they are feeding their young.

On the Variety of Land Birds. Although the land area is extensive, the number of different land birds (*i. e.*, birds of prey and passerine birds) is relatively small, consisting of 15 species, as follows: Turkey Vulture, Red-backed Hawk, Forster's Caracara, Southern Caracara, Peregrine Falcon, Short-eared Owl, Tussockbird,

Ground-tyrant, Short-billed Marsh Wren, Neotropical House Wren, Correndera Pipit, Falkland Robin, Red-breasted Troupial, Black-chinned Siskin, and Black-throated Finch.

The paucity of land species is attributed in a large measure to the persistently strong winds which have in turn limited the vegetational cover. There are no native trees. The principal plant cover for birds constitutes (1) grasses and low shrubs (6 to 12 inches high) on all the larger islands from low to moderate elevations; (2) high shrubs (up to 5 feet) along the banks of streams; and (3) tussock grass *(Poa flabellata)* along the coasts and over all the smaller islands that are more than bare rock. Tussock grows in dense clumps, sometimes 8 to 10 feet high, and on some islands — the so-called tussock islands — the clumps are so close together as to blanket most of the surface above the high-tide line.

In or near settlements man has provided additional plant cover through a few successful tree and shrub plantations. The commonest tree is a conifer, the Monterey cypress *(Cypressus macrocarpa)*, which attains moderate size, and the commonest shrub is gorse *(Ulex europaeus)*, which is high and used for hedgerows, but in some places has escaped to produce thickets.

The plant offering the greatest protection from weather is the tussock grass and as a consequence it comprises the regular habitat for the most species: the Vulture, Forster's Caracara, Owl, Tussockbird, and the two Wrens. The grasses and low shrubs, which offer the least protection, are used regularly by only two species: the Pipit and Finch. The Robin, Troupial, and Siskin are tolerant of a wider variety of cover. Thus, the Robin nests in clumps of tussock, in trees and gorse, and occasionally on shelves of overhanging ledges and cliffs; the Siskin, in trees and high shrubs; and the Troupial on the ground, sheltered by grasses or shrubs of any height. All three of these species have profited by tree and shrub plantations. Only four species — the Hawk, Southern Caracara, Peregrine, and Ground-tyrant — require no vegetational cover, preferring cliffs and rocky slopes. All nest in exposed situations, except the Ground-tyrant which uses deep crevices beyond the reach of the wind.

The persisting strength of the winds has also caused a paucity of passerine species by limiting food supply, especially flying insects. Dragonflies, damselflies, mayflies, neuropterans, hemipterans, and homopterans are non-existent. One butterfly and a few moths are the only lepidopterans; one or two ichneumonflies and several parasitic wasps are the only hymenopterans. (Honey bees, though introduced on several different occasions by Falklanders, failed to survive.) Dipterans are represented by a few small flies and a blue-bottle fly *(Calliphora)* and coleopterans by several snout beetles and ground beetles, two or three carrion beetles, and a diving beetle *(Dytiscus)*. The principal insect food for birds occupying tussock areas are the very primitive, flightless camel-crickets *(Parudenus)*.

Besides limiting flying insects, the winds make their capture difficult. In order to obtain insects, the Ground-tyrant is compelled to seek them close to the ground, or in the lee of cliffs and hills.

For animal food, most of the passerine species rely heavily on other invertebrates such as spiders that occur in shrubs, particularly gorse, and amphipods that abound in dead kelp washed up on the beaches.

On Bird Populations. Just as the variety of land birds is small, so is the total population of each species. Habitats suitably protected against the winds occupy less than a third of the entire land surface; consequently no species is common everywhere. At the height of the nesting season one may walk miles over the rolling uplands of the two main islands without seeing a bird of any sort. Probably the Pipit and Finch are the two species most frequently observed, as their habitat of grasses and low shrubs is the most widespread; but they are never seen in impressive numbers. All species, with the exception of the Hawk, Southern Caracara, and Peregrine, tend to concentrate locally where there are optimum conditions of habitat and food. Without question, the places with the largest populations are the tussock islands and the vicinities of settlements. Yet even here there is no marked abundance of individuals such as one might note in a marsh or about settlements in a more favorable climate. There is good reason to believe that these places already hold the maximum number of birds that food and cover will support.

A further indication of the limiting effects of Falkland climate and weather is the absence of species that nest at the same latitudes in South America, 300 or more miles west. In southern Patagonia and Tierra del Fuego there are, for example, no less than 20 breeding passerine species (6 furnariids, 2 rhinocryptids, 5 tyrannids, 2 hirundinids, 1 icterid, and 4 fringillids) that have never become established in the Falklands. Now and then representatives of these species appear in the archipelago. I collected a Chilean Swallow *(Iridoprocne leucopyga)*, and such species as the Magellanic Babbler *(Scytalopus magellanicus)*, and Yellow-browed Finch *(Melanodera xanthogramma)*, have been reported by Bennett (1926). In view of the prevailing wind direction — from southern South America toward the Falklands — and the strength of the winds, it is entirely possible that all 20 species have accidentally reached the Falklands many times. The fact that they have failed to colonize can only be explained by either their inability to cope with the severity of the environment or their failure to compete successfully with species already established in the few available habitats.

On Migration. Although penguins, procellariiform birds, and shags tend to pull away from the islands after the nesting season, there is no marked fall exodus of other birds. Individuals of a few species form small flocks and show some seasonal movements. Chiloë Widgeons and Yellow-billed Teal sometimes proceed to harbors and coves following their nesting near inland ponds and streams; and Black-throated Finches move in small flocks over wide areas. But the majority of species seem to pass the winter in the same habitats where they nested. This is undoubtedly true of the birds living in tussock as well as birds along the coast. It seems certain that at least two coastal species, the Kelp Goose and Flightless Steamer Duck, remain in pairs on their territories the year round.

According to statements of a few authorities, four species regularly leave the Falklands to pass the winter in South America. These are the Winter Plover (ABBOTT, 1861; BENNETT, *op. cit*), Paraguayan Snipe (VALLENTIN, 1924; BENNETT, *op. cit.*), Falkland Plover (VALLENTIN, *op. cit.*), and Correndera Pipit (VALLENTIN, *op. cit.*). If these birds migrate to South America, as reported, they must necessarily cross 300 or more miles of open ocean against strong westerly winds. That these birds actually subject themselves to such a hazardous journey seems dubious. Until more information is obtained it is more reasonable to assume that they do not leave the islands but merely leave their breeding grounds, which are quite exposed, for sheltered valleys where they spend the colder months.

On the basis of the above observations and suppositions, one may conclude that the Falkland climate is never severe enough to force bird movement away from the islands, and that the strong westerly winds would have an inhibitory effect on migration, should it be attempted.

On Clutch-Size. As a result of severe climate and weather conditions, a considerable number of Falkland species have fewer eggs per clutch than do their close relatives in North America. (See Table 1.)

TABLE 1

*Comparative Clutch-Sizes of Falkland and North American Birds**

Rolland's Grebe	Horned Grebe, *(Podiceps auritus)*
1—3	4—5
Black-crowned Night Heron	Black-crowned Night Heron *(Nycticorax nycticorax)*
2—3	3—5
Chiloë Widgeon	American Widgeon *(Mareca americana)*
6—8	9—11
Yellow-billed Teal	Green-winged Teal *(Anas carolinensis)*
5—8	10—12
Falkland Plover	Semipalmated Plover *(Charadrius semipalmatus)*
2—3	4
Paraguayan Snipe	Common Snipe *(Capella gallinago)*
2	4
Short-eared Owl	Short-eared Owl *(Asio flammeus)*
2	5—7
Neotropical House Wren	North American House Wren *(Troglodytes aedon)*
4	6—8
Falkland Robin	American Robin *(Turdus migratorius)*
2—3	4
Correndera Pipit	Water Pipit *(Anthus spinoletta)*
4	4—5

* Data on Falkland species from VALLENTIN (1924), COBB (1933), MURPHY (1936) and the author's records; on North American species from A. C. BENT's »Life Histories of North American Birds» (1919—50).

The generalization has been made that the size of a clutch increases with latitude, implying that the farther away from the tropics birds breed, the more eggs they will have per nest. A widely accepted explanation for this phenomenon is that with

increased day length at the high latitudes birds have more time in which to gather food for their young and thus can rear larger broods. According to LACK (1954), clutch-size is hereditary and has evolved through natural selection »to correspond with the largest number of young for which the parents can, on the average, provide enough food». Clutch-size, then, is adapted to food requirements of the young, rather than to increased day length. It is noteworthy that these explanations are of clutch-sizes in altricial species which feed their young, not of precocial species whose young must gather their own food.

Falkland birds with small clutches range from strictly precocial species (*e. g.*, grebes, ducks, and shore birds) to strictly altricial species (passerine birds). That these small clutches are in all cases influenced by some common environmental factor, there seems little question.

In all probability the prevalance of small clutch-sizes stems from the severity of climate. MURPHY (1916), in accounting for the small clutch of the South Georgia Teal *(Anas georgica)*, believed that a smaller number of eggs can be more successfully incubated than a large number when the temperature is prevailingly cold. While this explanation may seem reasonable, it does not apply to comparable bird species in subarctic North America where clutch-sizes are invariably large.

I cannot escape the conviction that it is the low food supply resulting from climate and weather that is the main influence in the production of small clutches. I have already pointed out the low numbers of insects and other land invertebrates. I need only add that fresh-water food is also meager. Most ponds and streams are shallow, with muddy bottoms, and tea-colored water — that is, water that has been leached from peat and is highly acid. Aquatic plants are, consequently, few in variety and number. The two fish species, *Oplochiton zebra* and *Galaxias* sp., are small forms, sluggish, and nowhere abundant. Though I dipnetted several small ponds and streams I found only occasional diving beetles in various stages of development and small larval caddice-flies. All in all, these waters struck me as being rather lifeless.

All Falkland birds listed in Table 1 depend largely during the nesting season on the land and aquatic food to which I have referred, although the Black-crowned Night Heron, Falkland Plover, and occasionally some of the other species do resort to coastal situations where they can supplement their diet with the more abundant marine life. In any case, each of these species is confronted with the problem of obtaining sufficient food in a country where the food supply, through climatic causes, is deficient.

During the nesting season it is quite likely that these Falkland birds are unable to obtain enough food material for the physiological energies necessary to produce the larger clutches of which they may be genetically capable. The number of eggs laid in each nest is, therefore, determined not by heredity but by an environmental factor — low food supply resulting from a severe climate. In other words, small clutches in Falkland birds are due to unfavorable conditions at the time the eggs

are produced. This conclusion is given considerable strength through a recent paper by WAGNER (1957) in which the author demonstrated convincingly that small clutch-size in tropical birds is also due, in part, to unfavorable ecological factors at the time of egg-laying.

On Body Size. As the amount of heat lost by a bird is directly proportional to the surface area of the body, a larger bird has less difficulty in maintaining body heat than a small one because its surface area per unit of weight is less (PETTINGILL, 1956). It therefore holds that the larger a bird is, the more suited it is to living in a cold environment.

In the case of Falkland birds it is significant that at least six of the nine passerine species — Ground-tyrant, the two Wrens, Robin, Pipit, and Troupial — are larger than representatives of the same species on the adjacent South American mainland (HELLMAYR, 1927—37). Undoubtedly this development of larger size, which provides an obvious selective advantage, is attributable to the more severe climate of the Falklands.

On Miscellaneous Habits. The effects of wind on the habits of birds are in some instances favorable, in others unfavorable.

Turkey Vultures find the winds helpful as they search for food above coastal areas. On the many strong updrafts from winds deflected by cliffs and headlands these birds ride easily with little expenditure of energy.

Black-browed Albatrosses choose for their nesting areas the colonies of Rock-hopper Penguins and King Shags on the lofty cliffs and bluffs along the western coast of the archipelago. Though similarly situated colonies are on other coasts, these great birds with seven-foot wing-spreads select the western colonies because here the strong westerlies, arriving unchecked from the sea, are of greater assistance to their landings and take-offs.

Black-crowned Night Herons, long-legged with loose plumage, generally loiter, roost, and nest in thick bushes or tussock clumps in the shelter of cliffs or banks, away from the wind. But when searching for food at the water's edge they must cope with the wind, sometimes with great difficulty. Occasionally, in order to stand against the wind, they assume a pulled-down, pressed-in pose that offers as little resistance as possible to the oncoming force. Now and then they are actually blown off balance and must struggle to regain composure. Even though they customarily face the wind, their feathers are nonetheless ruffled, breaking the insulating layer of air between feathers and skin and thus causing discomfort through cooling.

Ground-tyrants, which generally catch insects while fluttering, jumping, and walking over rocks and grasses, are compelled to forage in the lee of the wind. When winds are especially strong, they move to deep gulleys or to eastern beaches under cliffs or embankments. But even here they are not beyond the reach of winds, particularly gales. As they invariably forage in the open rather than deep in tussock grass, the energy they necessarily expend in combatting the wind while feeding must be considerable.

The prevalance of strong winds appears to have no prohibitive effect on the flight-singing of Correndera Pipits. Once, while the wind was blowing close to gale force, I watched these small birds mount to heights of 75 feet or more and perform for long periods. The Paraguayan Snipes usually flight-perform regularly in the evenings and on moonlight nights. Unlike Common Snipes in North America, they did not perform at all during the daytime. I am inclined to believe that their habit of performing in the evening and at night is determined by the wind, whose force is usually reduced after sundown.

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SUMMARY

The Falkland Islands have a cool, remarkably equable climate the year round, with persistently strong, westerly winds. These peculiarities of climate and weather have pronounced effects on the 51 native species of breeding birds. Because the climate is equable, most species — except sea birds — have a long breeding season. The variety and populations of land birds are small, owing to the limitations inposed by the severe climate and winds on vegetational cover and food supply. Other than sea birds, few if any species migrate from the Falklands, since the climate is not sufficiently severe to force their exodus and since strong westerly winds would restrain their exodus, should it be attempted. A variety of species have small clutch-sizes, presumably the result of a low food supply. The majority of passerine species are larger in size than representatives of the same species on the adjacent South American mainland. This development is considered advantageous to birds in a severe climate. Winds have both favorable and unfavorable effects on certain habits of birds.

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Ornithological Explorations in North-eastern Asia

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The exploration of the bird fauna of north-eastern Siberia was started by me in 1931; now I am proceeding with my investigations. As a result of my fieldwork in the basin of the Anadyr River I published a monograph »The Fauna of the Anadyr Region», in 3 parts, 1939—1941. Then I set to work on the birds of the Chukchee (Chukotski) Peninsula and Wrangel Island. The monograph concerning this second series of explorations of north-eastern Siberia is prepared for print and I hope shall be published in the nearest future. At last I turned my attention to the bird fauna of the area lying south of the Anadyr region, the so called Koryak Highlands, the northern borders of which I visited in 1931 and 1932. The southern parts of this country remaining unexplored promised interesting results from zoogeographical point of view.

Last summer the Zoological Institute of the Academy of Sciences U.S.S.R. suggested I should explore the bird fauna in the vicinity of the village Tilichiki, situated on the shores of Korf Bay, in the northern part of the isthmus, forming the land bridge between Kamchatka and the mainland. The principal results of this trip to the shores of Korf Bay are briefly given in the present paper.

Koryak Land is intersected by a number of mountain ranges and river valleys; on the west and east it is bounded by sea. The landscape of the forest-tundra zone alternates here with tracts typical of the subalpine belt. The bird fauna of the highest central parts of Koryak plateau remains almost unknown. Judging from the species observed by me near Korf Bay on mountains not exceeding 1,000 m., the plateau must be inhabited by a well defined mountain and alpine fauna, which usually characterises great altitudes on vast mountaineous terrains. The river valleys support thickets of tall forest vegetation, which occurs also on the middle course of the Anadyr River. The sea shores, both high and low, with their bays and gulfs present varied and suitable conditions for sea birds, nesting sometimes in large colonies.

The high coast of Korf Bay and the plateau along the coastal strip near Tilichiki are elevated to about 30—50 m. a. s. l. A large area is covered here by meadow-tundra with shrubs scattered here and there, among which the alder and creeping

Fig. 1. The alpine and subalpine belts in the Koryak Highlands. Tilichiki, 5. VIII. 1957. Photo by L. A. Portenko.

cedar prevail. During my first excursion I was at once impressed by a wonderful resemblance (if not identity) of the local avifauna with the one I observed in Anadyr Land. *Oreopneuste fuscata* and *Budytes flavus* bred copiously in shrubs; *Turdus ruficollis eunomus, Lanius cristatus, Emberiza aureola* were common everywhere, and I found here *Emberiza pallasi*. On the adjacent parts of the tundra nested *Lagopus lagopus, Asio flammeus, Alauda arvensis* and *Calcarius lapponicus;* northward, in a more damp locality near the mouth of the Kultushnaya River, *Stercorarius parasiticus, Pisobia subminuta* and *Numenius phaeopus* were observed. Thereabout on small lakes waterfowl was abundant. I noted numerous *Gavia stellata, G. arctica, Podiceps griseigena, Oidemia fusca, O. nigra, Nyroca marila, Spatula clypeata, Dafila acuta, Nettion crecca, N. formosa, Larus schistisagus, L. ridibundus* and *Sterna hirundo;* waders — *Rhyacophilus glareola* and *Glottis nebularia* nested in the vicinity. I was surprised to obtain here in a treeless area ducklings of *Mergellus albellus*, which must have hatched under the cover of thick trunks of the creeping cedar. Such abnormal surroundings for an arboreal species may be explained by its penetrating beyond the extreme limits of its distribution. On small rivers I met with broods of *Mergus serrator* and *Actitis hypoleucos*. Of the birds of prey *Hierofalco gyrfalco* (coloured whitish), *Aesalon columbarius* and *Buteo lagopus* were observed; the latter species was more common than the two former ones.

From the zoogeographical point of view the fauna described may not be characterised as arctic, notwithstanding the presence of some tundra species. It certainly belongs to the forest-tundra complex, which has a continuous distribution throughout

Fig. 2. A general view of Koryak landscape at the mouth of the Kultushnaya River, 11. VIII. 1957. Photo by L. A. PORTENKO.

vast areas from the Anadyr basin south to the timber line of Kamchatka. In my former publications I distinguished this area inhabited by the mentioned ornithofauna as a peculiar zoogeographical subprovince of the Palaearctic Region and proposed to name it »Anadyr subprovince». The typical arctic bird fauna of the »Bering subprovince» extends south not beyond the Anadyr Range.

The forest-tundra fauna explored by me in the neighbourhood of Tilichiki, notwithstanding its close resemblance with that of Anadyr region, differs from the latter in some of its details. In Anadyr we have *Xenus cinereus, Hylocichla minima, Phylloscopus trochilus, Prunella montanella, Emberiza pusilla* etc. Not one of these species breeds in Koryak Land. At the same time we find here several invaders from the south: *Spatula clypeata, Larus schistisagus, L. ridibundus, Alauda arvensis* etc. Hence, there is every reason to distinguish a peculiar zoogeographical »Parapol subdistrict», which together with three other subdistricts I have named (PORTENKO, 1937 and 1958) »Anadyr of the Plain», »Markovo-Penzhina» and »Anadyr Alpine» compose, according to my scheme, the »Anadyr district».

The bird fauna confined to the subalpine and alpine belts of Koryak highlands represents an element of quite different affinities. The subalpine belt on the hillocks I investigated is very well defined. Patches of creeping cedar grow on stony soil covered with lichens. Luxuriant growths of bushes give shelter to numerous breeding species: *Calliope calliope, Turdus ruficollis eunomus, Acanthopneuste borealis, Acanthis flammea, Pinicola enucleator*. On a mountain stream running through those thickets I found a last year's brood of *Heteroscelus incanus brevipes*. The complex

Fig. 3 & 4. The Spoon-billed Sandpiper, *Eurynorhynchus pygmaeus* (L.). Tilichiki, 27. VIII. 1957. Photos by L. A. Portenko.

of species inhabiting the subalpine belt is very constant, although thickets of creeping cedar, enlivened by the presence of the above mentioned Warbler and Pine-Grosbeak, occur not only on the mountains but also on gently rolling plains.

The alpine belt even on hills of moderate elevation occupies very large areas. Rocky debris and mountain tundras prevail here, attracting *Lagopus mutus, Anthus spinoletta* and *Calcarius lapponicus*. It was in the alpine tundra I found a brood of *Calidris tenuirostris* and several families of *Oenanthe oenanthe. Buteo lagopus* and *Stercorarius longicaudus* were very common throughout the area. The breeding in Koryak Land of *Calidris tenuirostris* — the remarkable Wader peculiar to north-east Siberia only — indicates possible faunal relations between Koryak and Anadyr highlands. In Chukchee Peninsula I have never met with this species.

A few words about coastal birds. As a matter of fact, the arctic fauna extends south along the coasts of Chukchee Peninsula, the western and eastern shores of the Bering Sea, penetrating to the Comander and Aleutian Islands. Colonies of Cormorants, Kittiwakes and various Auks inhabit also the precipitous sea cliffs of Koryak Land. I had the leisure to explore only the lower parts of Koryak coast near Tilichiki, particularly the spit separating the lagoon from the sea and the mouths of two rivers. My ornithological finds from here proved to be of some value. First of all I had the luck of observing the wonderful *Eurynorhynchus pygmaeus* on its breeding grounds, and to meet with a representative of the American fauna — *Limnodromus scolopaceus* and with such a rarity as *Sterna camtschatica* (= *S. aleutica*) as well. *Limonites temminckii* was also found nesting. None of the mentioned birds are strictly speaking arctic. On the other hand, such northern species as *Philacte canagica, Larus hyperboreus, Sterna paradisaea, Arenaria interpres, Pisobia ruficollis* and others, which breed near the mouth of the Anadyr River, are absent from Korf Bay. *Eurynorhynchus pygmaeus, Limnodromus scolopaceus* and *Limonites temminckii*, according to my data, find near Korf Bay the southern limit of their distribution.

Our ornithological explorations in north-eastern Asia have greatly increased our knowledge on the bird fauna of this region, but we certainly may not consider them final. Many new discoveries and interesting findings may yet be expected in future. In any case, the general scheme of the distribution of birds in the country explored is now cleared up.

My ornithological works in 1957 led me up to a very important conclusion, that the Koryak Highlands are inhabited almost by the same ornithofauna as in the basin of middle and lower course of the Anadyr River. Thus the fauna of the forest-tundra here dominates throughout a very extensive area — latitudinally much the widest in the whole Eurasia. The admixture of typically arctic species in this forest-tundra complex is very poor; of forms characteristic of the Kamchatka fauna only several subspecies may be named; American elements are insignificant. The principal faunal background of Koryak Land is formed by species peculiar to the mainland of eastern Siberia.

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Vocal Imitations in Some Birds

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In recent years much work has been done on problems concerning the voice of birds. Many questions have been studied, such as description of the vocabulary of calls of a certain species, the external and internal factors eliciting them, their function as a language, their ontogenetic development, analysis of the sounds, their dependance on inheritance and learning, and so on. Studies on birds reared in isolation from other birds of the same species have revealed that in for example, the White-throat *(Sylvia communis)* according to Sauer (1954), the Blackbird *(Turdus merula)* according to Messmer (1956) and the Canary *(Serinus canaria)* (Poulsen 1959) the song does not have to be learnt from other birds of the species.

Call-notes seem in general to be inborn. This is for instance true of the whole repertoire of calls in the White-throat, the Blackbird, the Chaffinch and the Canary, but exceptions exist, for instance the call-note and the alarm-note in the Goldfinch *(Carduelis carduelis)* and two social calls in the Bullfinch *(Pyrrhula pyrrhula)* according to Heinroth (1926) and the flight call of the Linnet (Poulsen 1954).

In some species the song has an innate basis, but the complete song must partly be learnt. This is the case with the Chaffinch *(Fringilla coelebs)* (Poulsen 1951, Thorpe 1954), the Linnet *(Carduelis cannabina)* (Poulsen 1954) and the Pied and the Collared Flycatcher *(Muscicapa hypoleuca* and *M. collaris)* (Löhrl 1955).

Species which acquire their full song by learning from birds of the same species only imitate during certain short periods of their life: as juveniles and when they are one year old, and then their song — or songs — has become fixed, *e. g.* the Chaffinch (Thorpe *l. c.*) and the Linnet (Poulsen *l. c.*). Other species imitate parts of song and calls of other species and incorporate them in their own song and do this all through their life. Such mocking-birds are *e, g,* the Starling *(Sturnus vulgaris)*, the Red-backed Shrike *(Lanius collurio)*, the Blue-throat *(Luscinia suecica)*, the March-Warbler *(Acrocephalus palustris)*, the Indian Grackle *(Gracula religiosa)* the Shama *(Kittacincla macroura)*, the North American Mockingbird *(Mimus polyglottus)*, the Shell-parakeet *(Melopsittacus undulatus)*, and other parrots, which also imitate sounds other than animal calls, *e. g.* knocking at doors, water drops falling into water, and noise from machines.

Whereas these birds normally include imitations in their full song, other species which have proved to be able to imitate alien songs nevertheless do not normally in the wild have imitations in their song. This for instance happens in the Linnet *(Carduelis cannabina)*, the Siskin *(Carduelis spinus)*, the Bullfinch *(Pyrrhula pyrrhula)*, and the Domestic Canary *(Serinus canaria)*.

The Canary, in which the song does not have to be learnt, sometimes has imitations besides its own song, *e. g.* phrases of the Grey Singing Finch *(Serinus leucopygius)*. The Canary never picks up imitations when it is singing its full song, but only when singing the low motivated subsong. It is not able to imitate alien songs at all times, but only in the period in autumn in which it sings its subsong both as adult and as young bird; even youngsters seem to learn (POULSEN 1959). The imitations, which may be complete copies of the alien song, are never interspersed in its own song, but are given before or following it.

Independent of this imitation of alien songs in the subsong period some individuals imitate the alarm and the social call of the Song Canary — a domestic strain in which the song and other calls are of a lower pitch, and this learning does not seem to be restricted to the subsong period.

Thus there seems to be a connection between learning and subsong in the Canary. The song motivation in the subsong period is low, and the song does not have a strict pattern, but is more flexible and is delivered intermittently. The bird is not excited as when singing towards females and rivals, and the song is apparently without any function.

In many species song is a loud articulated sequence of sounds easy to locate and functioning as a proclamation of the territory of the singer, repelling males and attracting females. In such a species as the Bullfinch *(Pyrrhula pyrrhula)* the song is not loud, and it does not seem to have a function. This bird does not seem to be territorial and it is never seen countersinging a loud, clear song with other males. At their breeding grounds it is heard singing the same song as in winter and early spring. In captivity some adult Bullfinches pick up song phrases and calls of other species, *e. g.* the Canary. The Bullfinch has long been known as a good imitator. Young birds taken out of the nest and raised by hand learned to sing alien birdsongs or melodies taught them by humans. In captivity some Bullfinches also as adults pick up song phrases of other species. This is certainly connected with the subsong-like song this species has nearly all through the year — at least in captivity. I have had an adult Bullfinch which imitated the alarm call and parts of the song of the Canary. Its song was interspersed with song phrases of the Canary in an irregular sequence (Fig. c).

The Siskin *(Carduelis spinus)* has a lively twittering song terminating in a prolonged creaking note which is given from trees and in songflights in the breeding time. Outside the breeding time a more or less subdued subsong without end-note is to be heard, and males are often singing in chorus in flocks. In captivity song is heard most of the year. The song is given in the breeding time while chasing other

males and in display towards females, but it is not known if the Siskin is territorial or not.

In the subsong period the adult Siskin sometimes imitates alien song phrases, for instance I once had a Siskin which imitated parts of the song of the Canary, different song phrases being inserted in its own song, but never in a distinct sequence (Fig. d).

The song of the Bullfinch is innate according to HEINROTH *(l. c.)*, but nothing is known about the song of the Siskin, and as already mentioned the song of the Canary is inherited, but nevertheless these birds have an ability to imitate.

The Chaffinch and the Linnet, which partly have to learn their songs, also do not normally imitate other species, but certain Linnets reared by hand and later on kept together with other species do so (Fig. b). The Chaffinch, which may include imitations in the subsong of the young bird, drops them in the true song according to THORPE (1955), and adult Chaffinches are never heard imitating other species.

The mimicry by species which are not normally recognized as mimics may be an abnormal condition due to captivity. Cage birds have more leisure to give their attention to sounds around them. But the records of captive birds show that these species do have a song-learning faculty.

Thus, even birds in which the song is innate, *e. g.* the Bullfinch and the Canary, besides have a »luxury» song-learning faculty which normally is not used. It may be mentioned that the Black-bird in which the full song is innate normally incorporates imitations from other Black-birds in its song (MESSMER 1956).

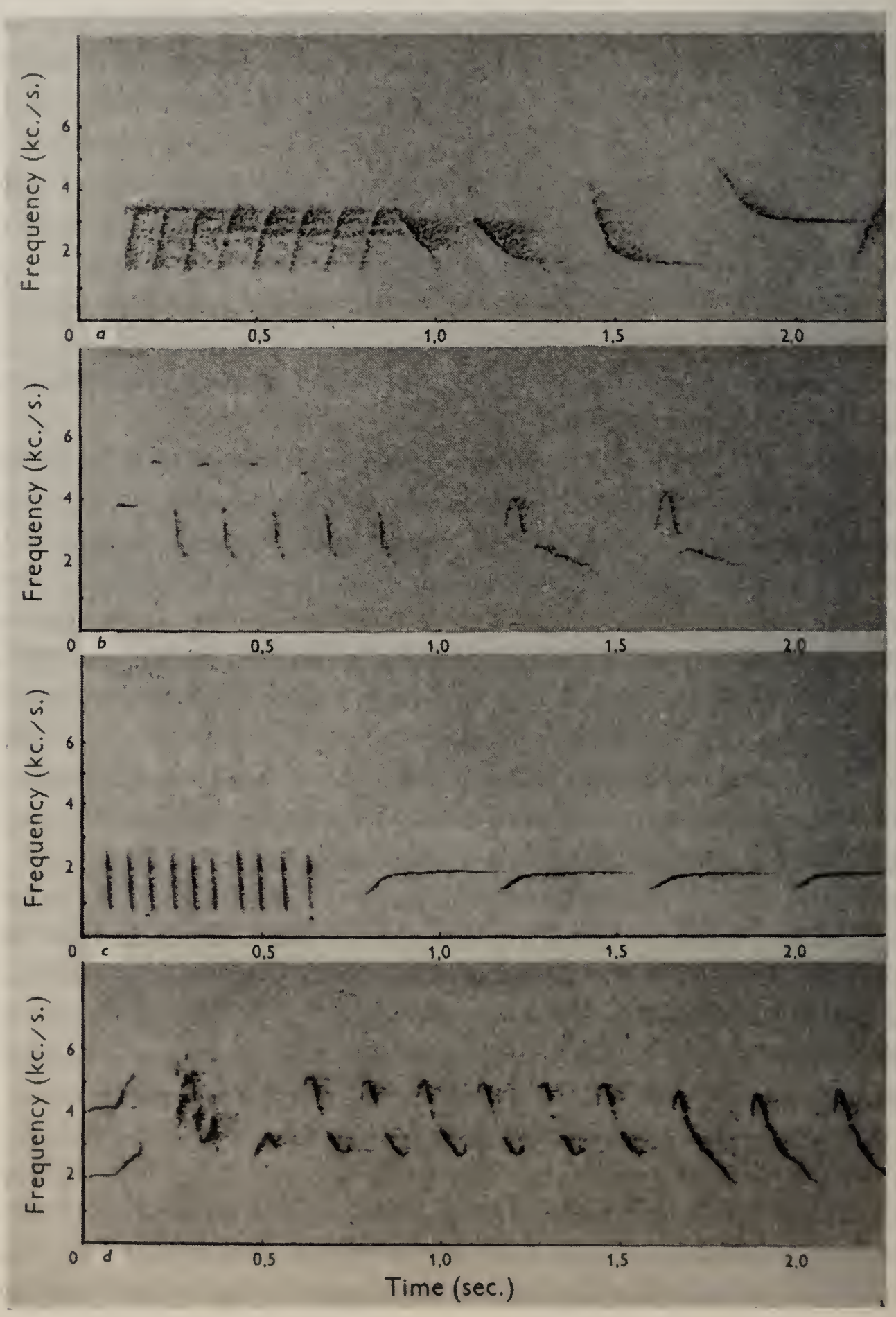
It has not yet been investigated how many songs a bird must hear or for how long before it imitates it. The shortest learning period I have experienced is 5 days for a Canary to learn a song phrase from a Song Canary. Nor is it known whether a bird which is learning an alien song gives more or less incomplete imitations at the beginning and subsequently make them conform better to the original, or whether it gives the imitation complete and suddenly after having been exposed to the alien song for some time. In the Canary the latter seems to be the case.

In species in which the song is not completely inborn there seems to be a preference for imitating the specific song pattern, *e. g.* in the Chaffinch and the Linnet. When they are exposed to songs of many species they adhere to the song of their own species. Single Canaries which are kept together with many other species are inclined to imitate certain species which have a song with certain similarities to their own song such as trills and whistles of about the same rhythm and pitch.

The imitations are often very like the original. For instance in a Canary's imitations of the call-note and the song of the Song Canary the pitch is lowered and the rhythm is slowed down untill it conforms to the pattern of the original (POULSEN 1959).

What happens to the learned songs in the course of the life of the bird? When a Chaffinch or a Linnet has acquired its full song it is never altered in later years. But the extra imitations of alien songs which occur in Canaries disappear if the bird is exposed exclusively to the song of its own species later on. If they are kept alone

they retain the mimicked sounds for years. In the two first-mentioned species learning is superimposed on the innate song. This song learning involving the perceptual process of recognizing the song of the species (or a similar song), the acquisition of the new motor patterns in performing the song and the learning restricted to certain periods, seems to resemble the type of learning called imprinting.



Sonograms of one phrase of the song of the Domestic Canary: *a*, and of the imitations of this phrase in the songs of Linnet: *b*, Bullfinch: *c*, and Siskin: *d*.

The species dealt with here are not what we call mocking-birds, which normally in their wild state mimic sounds of other species and probably do it at any time of their life. At present one cannot see any biological significance in this vocal imitation. In many cases it seems to be imitation for its own sake.

Especially in species in which the song and other calls are innate it seems inexplicable that the birds are also able to utter copied notes. None of the species described here has shown any signs of improvisation in their singing, which is the case with the more generally imitative species which are more proficient as songsters.

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The Influence of the Wind on the Migration of Swallows

Ottenby Bird Station Report No. 26

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Migratory movements in birds normally occur at more or less restricted periods outside the breeding season. The Swift *(Apus apus)* constitutes an exception to this rule. In this species such movements seem to occur during any time of the year, including the breeding season, as has been shown by Koskimies (1950) and Svärdson (1951). The selective advantage of such behaviour is indicated because Swifts depend entirely upon the number of airborn insects, which vary in abundance with changes in weather conditions. Sedentary habits may seriously jeopardize these birds during extended periods of bad weather. Koskimies has shown that Swifts avoid the bad weather of a cyclone by a »weather flight». The birds then fly against the wind, thus moving away from the center of the cyclone.

Even if the dependence of air plankton is stronger in the Swifts than in other birds, the adaptation of the swallows has followed the same general trend. Their sensitivity to the weather may be illustrated by the »swallow catastrophes», resulting from a sudden outbreak of bad weather (see *i. e.* Lorenz 1932). Although swallows seem to be sedentary during the breeding season, some observations indicate that weather movements comparable to the ones found in Swifts might occur (Lack 1956). This is supported by the following observations made at Ottenby Bird Station in Sweden in the fall 1947. During a period of observation of one month from August 16th to September 15th there was an almost constant northern wind from August 18th to September 4th. General migrational activity practically closed. The only species flying in large numbers were swallows and Swifts. 10,000 birds of these species were recorded flying northwards against the wind during this period. This flight was observed every day except one, reaching a maximum on August 22nd and 23rd, when close to 2,000 individuals were recorded per day. The majority were House Martins *(Delichon urbica)*, which constituted over 90 per cent of the total records; 4 per cent were Swallows *(Hirundo rustica)*, 3 per cent Sand Martins *(Riparia riparia)* and 2 per cent Swifts *(Apus apus)*. During the same period only 200, still mainly House Martins, were observed migrating in the »correct» southward direction with

a tail wind. This occurred at the end of the period, September 2nd. Before and after the period of northern winds, that is, August 16th and 17th and September 5th to 15th, the prevailing winds were from a direction between south and west. A southward migration of swallows was then observed. 5,200 birds were recorded, 36 per cent *Hirundo rustica*, 33 per cent *Delichon urbica* and 31 per cent *Riparia riparia*. With the exception of a few individuals, no Swifts took part in this migration.

On August 18th there was a cold front along the Baltic from Finland to Denmark and a low pressure area over western Russia east of Finland. A stationary area of high pressure in the western part of Scandinavia and the passage of cyclones southeast of the Baltic were the cause of the following period of northern winds. During the period in question the weather was clear, showing the characteristics of the »back» of cyclones. This weather situation influenced a large part of Sweden and in fact similar northward movements of swallows were reported elsewhere (Svärdson 1948).

In the Swift, northward flights, according to Koskimies, have been observed predominantly in the northwestern sector of the cyclones, when the birds were returning to their summer localities after a weather flight. The observations at Ottenby indicate that similar behaviour may occur in swallows during ordinary migration. The northward movement in this case was presumably caused by the reaction of the birds to the winds.

Recognizing the difficulties in determining the direction of the flight of swallows and Swifts, observations were made as accurately as possible by using class intervals of 22° or N — NNE — NE etc. There was a marked correlation between the direction of the flight and the wind, as can be seen in fig. 1, illustrating deviations of the flight of the swallows from the wind direction.

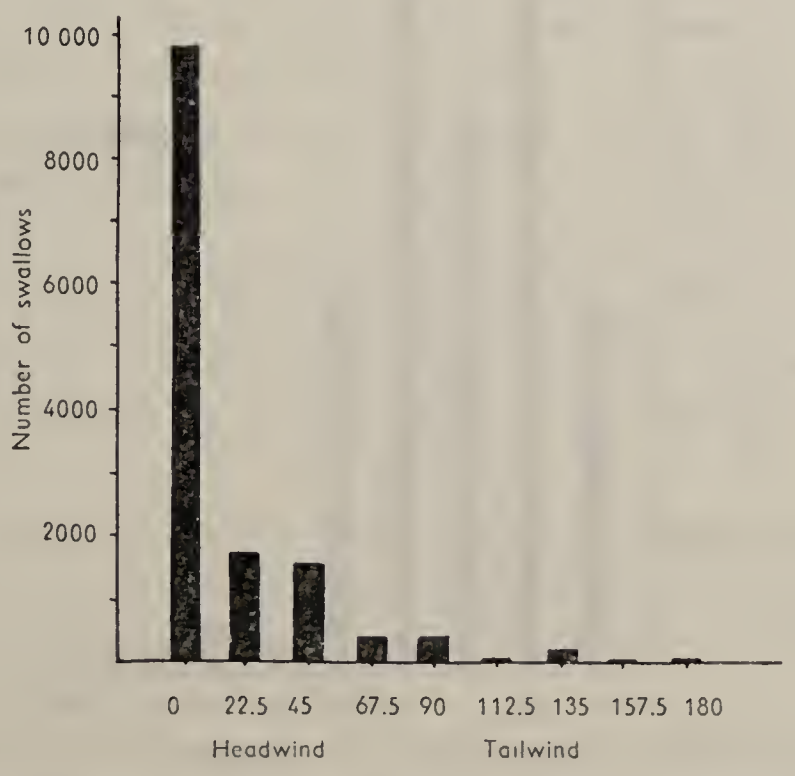

Fig. 1. Deviation (in degrees) of the flight of swallows from the direction of the wind. Ottenby August 16th to September 15th 1947.

In order to study to what extent this reaction towards the wind is a general feature under ordinary circumstances, studies were made the following year at Falsterbo Bird Station at the southern point of Sweden from July 31st to August 15th. The topographical conditions are somewhat better here for such a study than at Ottenby, where the narrow tip with the coast lines, running in a north-south direction, may restrict the choice of direction of the birds by means of the guiding line effect. The direction of the wind varied considerably and the weather situation was in general more normal than at Ottenby the preceding year.

During the period at Falsterbo 6,600 swallows and Swifts were observed. The proportions of the various species were different from those observed at Ottenby 1947, the Swifts being in the majority with 64 per cent, whereas *Riparia riparia* occurred to the extent of 20 per cent, *Hirundo rustica* 10 per cent, and *Delichon urbica* 6 per cent. The preference for flying against the wind was still marked, as can be seen in Fig. 2, where the deviation of the direction of the flight from the wind is recorded.

The hour of the day when migration of swallows and Swifts occurs seems in general to be less restricted than for most other birds, the time being determined to a large extent by the occurrence of favourable winds. Assuming an average direction of flight towards the southwest at Falsterbo, there were only four days which showed a complete lack of winds giving a head wind component. The only return migration of noticeable magnitude occurred on one of these four days. 460 birds, mainly Swifts, took part in this flight.

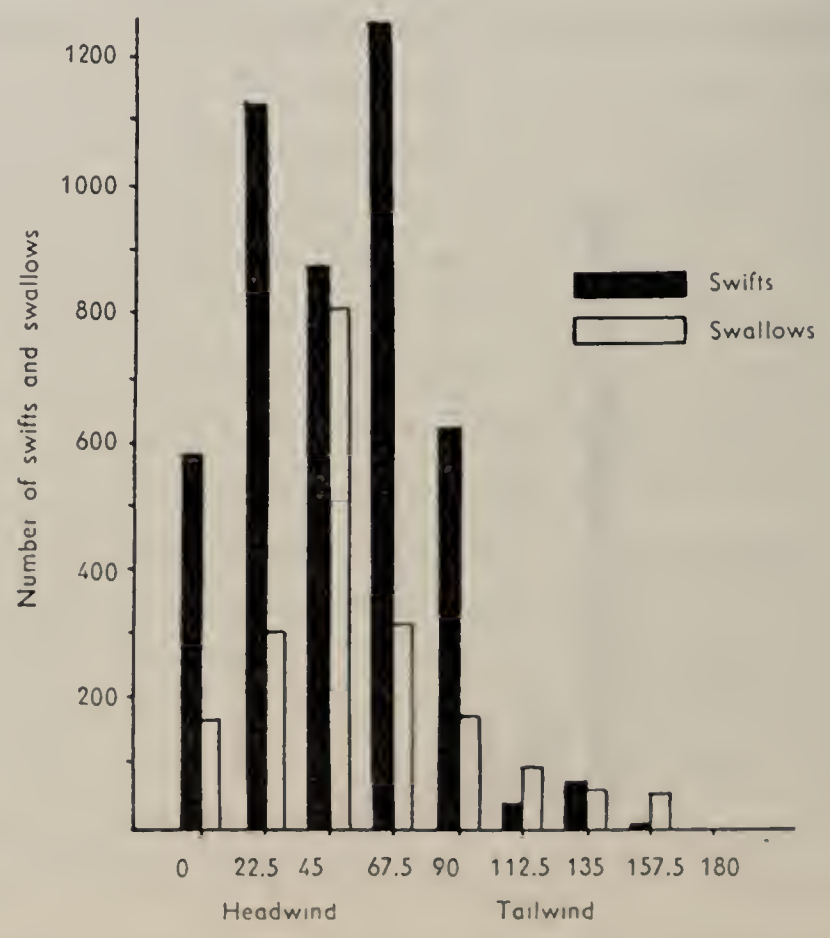

Fig. 2. Deviation (in degrees) of the flight of swallows and Swifts from the direction of the wind. Falsterbo July 31st to August 15th 1948.

The reaction of the Swifts and the swallows towards the wind could be interpreted as an adaptation to avoid areas of low pressure, as has been suggested by KOSKIMIES for the Swifts. It seems, however, likely that the wind exerts a direct aerodynamical influence on the flight, as a similar reaction in fact does occur in other bird species as well. At Ottenby the birds of prey showed a reaction to the wind, which was somewhat similar to that of the swallows. 188 birds of prey were recorded during the whole period from August 16th to September 15th. The direction of their flight was as follows:

	Southward	Northward
Falco peregrinus	6	1
» *subbuteo*	1	7
» *columbarius*	17	4
» *tinnunculus*	18	25
Accipiter nisus	33	33
Circus aeruginosus	7	2
» *pygargus*	2	—
Pernis apivorus	8	—
Pandion haliaetus	23	1
Total	115	73

Of the 73 observations of northward flight, 69 occurred during the period of northern winds. During the same time only 21 migrated southwards.

Although the effect of horizontal winds on bird flight has been a controversial matter, a number of observations recorded in the literature on the tendency of many species to fly against the wind, together with data on reverse migration against the wind, indicate that the wind direction is of aerodynamical importance. NISBETH (1955) has pointed out that the asymmetrical distribution of the velocity variations of the wind, with largest sudden changes in the downwind direction, makes flying safer against the wind, there being less danger of aerodynamical instability due to sudden falls of air speed below the stalling speed. A bird flying with a tail wind therefore ought to avoid high wind turbulence which often is found at low levels. This would explain the general tendency of birds to fly at higher altitudes with a tail wind. Of some interest in this connection is an observation by SCHWERDTFEGER (1942). He saw from an airplane a flock of geese migrating with the wind at an altitude of 2,600 m. The occurrence of the birds at this high altitude was explained by the fact that there were turbulent air currents at lower levels, which were avoided by the geese.

It is likely that soaring and gliding birds are especially sensitive to winds causing changes of air speed below the stalling speed. Such winds would force these birds to use a more energy-consuming type of flight, particularily over large areas of water, where no thermic up-currents are available.

The strong anemotactic behaviour of swallows and swifts may be explained by the following circumstances. The size of a bird constitutes a limiting factor for a gliding flight technique (LORENZ 1933). Swallows and Swifts show an extreme adapta-

tion to a gliding flight, being the smallest birds using such a technique, the consequence of which is that they probably are more sensitive to air currents than other species using a similar kind of flight. It is furthermore possible that a flapping flight technique interferes with their ability to catch insects. A gliding flight technique becomes increasingly more difficult the more often the air speed decreases below the stalling speed, which presumably occurs especially in wind gusts in the downwind direction.

An important factor in this connection may be the feeding behaviour of swallows and Swifts. While other birds on migration ordinarily feed while resting, these species feed to a large extent at the same time as they migrate (comp. HURRELL 1937). They therefore have to remain at an atmospheric level, within which there is an abundant supply of airborn insects, usually below 300 m. (see KOSKIMIES op. cit.). Their possibility of correcting the altitude of flight according to the distribution of different air currents is therefore restricted. Northern winds with a weather situation which releases the migration may thus force them to migrate in a direction opposite to the normal one, assuming an influence of horizontal winds outlined above.

It may be noted that several recoveries of ringed swallows and Swifts have been made north of the place of ringing the same autumn. DROST and DESSELBERG (1932) have interpreted such recoveries of *Hirundo rustica* as a result of »Zwischenzug». It seems, however, rather likely that such northward flights in most cases are a part of the true migration, although temporarily in a reverse direction. As a matter of fact both young and adult specimens of *Hirundo rustica* were observed at Ottenby on northward migration.

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Distribution and Niche Differentiation in Species of Megapodes in the Moluccas and Western Papuan Area

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In 1954, I had the good fortune to return to the Moluccas and Western Papuan area with my wife in order to collect and observe birds. Our trip was made possible by generous assistance from the Governments of Indonesia and Netherlands New Guinea, to both of which I must express our gratitude. In addition, I was fortunate enough to receive grants from the Guggenheim Foundation and the National Science Foundation. To these organizations we are much indebted.

One of the bird families which we studied was that of the Megapodes. These strong-footed, largely terrestrial galliform birds, whose eggs hatch independently in mounds and in which there is no parental care of the young, have their centers of distribution in the Papuan area. Several of the species are little-known in habits and ecology. Much of what is known of them has been ably summarized by Frith (1956). We were fortunate enough to encounter four species during our stay: *Eulipoa wallacei, Megapodius freycinet, Talegalla cuvieri,* and *Aepypodius arfakianus.*

EULIPOA

Eulipoa is a monotypic genus of megapode found in the Moluccan Islands. It is very close in size to *Megapodius*. The wing measurements of *Eulipoa* average perhaps ten millimeters less (a difference of only 5 per cent in total length) than in *Megapodius*, the tarsus between 4—5 millimeters less, and the culmen is fractionally smaller. There is no perceptible difference in bill size or structure.

Eulipoa occurs in islands in the Moluccas, having been recorded from Halmahera, Ternate (possibly an error as this may have been a »trade skin» secured on a neighboring island), Batjan, Ceram, Haruku, Ambon, and Buru, all islands with high mountains. Normally, the species occurs above 300 meters in altitude, usually higher, from 750 meters up to 2,000 meters. However, during the time of laying, *Eulipoa* resorts to the sea beaches where, in certain favored localities, an egg is laid in a hole in the sand. These sites have been well described (Toxopeus, L. J., in Siebers,

1921—1922; and HEINRICH, 1956). HEINRICH *(op. cit.)* collected a female at 1,500 meters altitude on Batjan in June which had a hardshelled egg in the oviduct ready to be laid. Whether such a bird could make the journey down to the beach in time to lay the egg during the night (when the eggs are deposited in slanting tunnels dug in the sand) or whether she could not have reached the beach is indeed an interesting speculation. TOXOPEUS *(op. cit. : 38)* suggests that the female *Eulipoa* occasionally lays an egg in the humus nest mounds of *Megapodius* in the forest. The fact remains, however, that *Eulipoa* primarily resorts to special spots on the sea beaches in an entirely different altitudinal zone from its normal habitat. Furthermore, the trip to and from the egg laying area is performed at the last moment as HEINRICH has reported *(op. cit.)*, and the local inhabitants have always related.

Another megapode, *Megacephalon maleo*, on Celebes similarly leaves its forest habitat and visits coastal beaches to lay. The young on hatching find their own way by kicking themselves out of the sand tunnels and presumably half walk, half fly up to their specific altitudinal habitat, although no information is available on the time it takes them to reach their home range.

BREEDING SEASON

The egg deposition period for *Eulipoa* is incompletely known. TOXOPEUS *(op. cit.)* found birds laying eggs on the beach on Buru in December as well as a young hatching, indicating a similar breeding season to *Megapodius*, *i. e.*, September to December. HEINRICH found an oviduct egg, on the other hand, on June 29. Male specimens taken by us had somewhat enlarged gonads in October and November.

Beyond seeing *Eulipoa* on Batjan Island at altitudes ranging from 2,500 feet to 5,500 feet in dense evergreen rain forest and subtropical wet moss forest during October, we would have had little to add to these previous notes. We found *Eulipoa* on Batjan only at higher altitudes on the slopes of Mount Sibela, always at the upper limit of the range of *Megapodius*, although we did find an old humus-nest mound of *Megapodius* as high as 2,000 feet. However, all our observations confirmed previous reports that, except for the period of egg deposition, the two megapodes, *Eulipoa* and *Megapodius*, occupy altitudinally separated ranges in the Moluccan Islands. *Megapodius* is common in mangrove and lowland wet evergreen forest from the sea shore to 300 meters, rarely higher, while *Eulipoa* is found in the hills above 300 meters except for egg laying.

However, when we reached the island of Misool, one of the western Papuan Islands, we again, to our surprise, encountered *Eulipoa*.

Misool is still not a well-known island faunistically. CHARLES ALLEN made a short stop there for ALFRED RUSSELL WALLACE in 1861. WATERSTRADT collected on Misool for the Tring Museum in 1902, and I had visited the island for a short time in 1937 (MAYR and DE SCHAUENSEE, 1939). Misool is on the Sahul Shelf, on which

New Guinea lies, within the 200 meter line, and is considered to belong to the Papuan Region rather than to the more transitional area of the Moluccas to the west. However, we found *Eulipoa* on Misool in 1954, a new record for that island, thus showing that although Misool is on a shallow shelf, it has been isolated for a long time from the New Guinea mainland. We collected two male *Eulipoa* at low altitudes (approximately 300 feet above sea level) indicating that the species on this island is not altitudinally separated from *Megapodius*. It appears to be a rare bird. Most Arafura hunters do not know it or, if they do, speak of it as very rare. The Arafura name I was given for *Eulipoa* was »holeiko». *Megapodius* is common on the island, which has only a small range of tumbled limestone hills in the south-central part, barely reaching 800 meters elevation, not sufficient to allow for any altitudinal zonation. It seems difficult to believe that Misool can really present anything but a homogenous environment.

From a zoogeographic point of view, the occurrence of *Eulipoa* on Misool points again to the currently accepted thesis that the island marks a stepping stone in an ancient link between Ceram to the southwest and New Guinea (Rensch, 1936; de Beaufort, 1951). Ceram is the only Moluccan Island to share the cassowary with New Guinea, a markedly distinct subspecies. It also possesses an endemic genus of Marsupial bandicoot. It is interesting in this connection that Misool lacks the cassowary along with other offlying western Papuan islands, although the possibility should not be discounted that human hunting pressure within historic times may have exterminated the species on these easily accessible peripheral islands. In any case, it seems extraordinary to find this endemic species of megapode of the more depauperate fauna of the Moluccas on one of the western Papuan islands within the dispersal area of the richly productive New Guinea fauna.

The genus *Eulipoa* is characterized by Ogilvie-Grant (1893) as differing from *Megapodius* in having the secondaries much shorter than the primary quills, while in the latter the secondaries are as long as the primary quills. In those specimens which I have examined, this character is not apparent. Indeed, it seems to me that there is no structural difference in these two genera. The only obvious differences are that *Eulipoa* appears to share with *Megacephalon* an interesting behavioral character, different from other Megapodes, of reverting to the coastal sand beaches from its upland habitat for egg deposition. *Megapodius*, which may lay in the sand, as well as construct humus nest mounds, does not normally perform a vertical migration to do so. In addition, *Eulipoa* has a distinctive pattern of color in the plumage, the scapulars and back feathers banded with bright chestnut, the primaries and secondaries with buff spots, and the lower belly and vent white. No species of *Megapodius* has such a bright and distinctive pattern, although some, *i. e.*, *duperreyi*, show a tendency towards the gray, olive, brown, or chestnut tones of *Eulipoa*. It seems to me then to be debatable and open to question whether *Eulipoa wallacei* deserves to rank as a monotypic genus or be merged as a strongly marked species of *Megapodius*.

MEGAPODIUS

Megapodius freycinet is distributed from the Nicobar Islands through the Sunda Islands to the Moluccas, New Guinea, northern Australia, and the New Hebrides. As FRITH says (1956, *op. cit.*) it is a young and vigorous species that is differentiating taxonomically as well as ecologically. On the Moluccan Islands, *Megapodius* appears to make humus mound nests in the forests, and not to lay on the sea beaches as the species does in the Solomon Islands.

On Misool, as on the other off-lying western Papuan Islands, *Megapodius freycinet* is common. It occurs all over the island and may nest on the edge of the beaches or in the center of the island.

SPECIATION TRENDS

From what is known of the Moluccan fauna, it would be logical to assume that *Eulipoa* is the older, first invader of the area in time, its arrival coinciding perhaps with the pre-pleistocene emergence of these islands. Misool is presumably an old feature in the distribution of animal life arriving from the Papuan-Australian region. *Eulipoa* is conservative in that it has not differentiated into morphologically recognizable populations, even though isolated in a discontinuous distribution.

Megapodius has split into several discrete populations throughout its vast range, although only one is recognized in the Moluccan-West Papuan Island area, implying that its distribution is a fairly continuous one, and relatively recent in time.

SPECIES COMPETITION

It would appear as if *Eulipoa* and *Megapodius*, closely related as they are, and of nearly identical size, were in potential competition. If the requirements of two species are sufficiently similar, the proposition of VOLTERRA (1926) and GAUSE (1934) suggests that only one will be able to persist. Nothing is known about differences in food or space requirements which would suggest that these two species would not be in competition should they coexist in the same biotope. The previously known distribution of these two species, altitudinally separated in the Moluccas, presumed that they were not in competition. LACK (1944) has pointed out that the chance is negligible that, after their differentiation in isolation, two species should be equally well adapted in every way and thus that it would be inevitable that only one species would survive. And yet, here on Misool two very similar species coexist, both in this area, presumably adapted for similar niches. It seems unlikely, as I have stated above, that Misool with its extremely limited area of low hills can represent anything but a homogeneous environment for these species.

As *Megapodius* is the common species on Misool, and *Eulipoa* is apparently extremely rare, several possibilities emerge:

A. *Megapodius* and *Eulipoa* are not really in competition. Without more detailed knowledge, this possibility cannot be proved one way or the other. The fact that in

other localities the species are altitudinally separated suggests, however, that they are potentially in competition.

B. *Megapodius* and *Eulipoa* are in competition. If these two species are in competition, then their being sympatric on Misool can be explained in the following ways:

1. As CROMBIE (1945) has pointed out in insects, the results of competition between different organisms may vary with the conditions under which they occur. A stage of ecological succession may be in progress here in which *Eulipoa* has in fact become extremely rare in this environment, as conditions are changed by the presence of *Megapodius*. This implies an actual change, presaging the extinction of *Eulipoa* on Misool. By chance, we might have been witnessing the elimination of one species by another, a process *in statu nascendi*. The fact that these species are both old and well established in the whole area militates against this supposition.

2. *Megapodius* and *Eulipoa* may each be inhibiting their own population increase. MACARTHUR has pointed out (1958) that to permit coexistence it seems necessary that each species, when very abundant, should inhibit its own further increase more that it inhibits another's. Differences in food, spatial requirements and so forth do not always seem necessary or sufficient to prevent competition under conditions of complete sympatry. In view of their distribution elsewhere, this explanation does not seem plausible.

3. *Megapodius* and *Eulipoa* are being kept at a low population level relative to the environment by extrinsic, density independent factors. I believe that some explanation of this sort is conceivable. Predation pressure must be heavy on Misool whose human population is considerable. The indigenous Arafuras are active hunters, rather than coastal fishermen and cultivators as are the Besarese. The nest sites and the nesting seasons of the species of megapodes are well known. Arafura dogs visit the mounds and presumably the beaches. Other predators such as *Varanus* should not be overlooked.

I would suggest then that *Eulipoa,* the presumed first arrival on Misool has been prevented from becoming subject to severe competition by *Megapodius,* because the populations of the two species have been held at a relatively low level by density independent factors. One obvious factor readily observable is that of predation. A kind of equilibrium has been reached without the two species having reached a maximal population level. The geographical distribution of the two species is summarized in Figure 1.

TALEGALLA

Talegalla is a large mound-building bush turkey found in coastal areas of western New Guinea and the off-lying western Papuan and Geelvink Bay islands. It has been known to occur on Misool where we encountered it in the typical wet evergreen forest in all parts of the Island. It is a large bird, the size of a small turkey. In New Guinea it does not range higher than 800 meters into the mountains.

Fig. 1. Comparison of the geographical ranges of *Megapodius* and *Eulipoa*. On the islands where they occur together, the two species are presumed to be altitudinally separated, except on Misool.

AEPYPODIUS

This large mound-building megapode occurs in the mountains of New Guinea above 1,000 meters and is altitudinally separated from the preceding species *contra* FRITH *(op. cit.)* who states that species of both genera may occur in the same area.

Aepypodius is virtually identical in size with *Talegalla* (wing averages about 5 per cent smaller) and builds roughly similar, though somewhat larger, mounds, a description of which may be found in MAYR (1930). *Aepypodius* has been generically, separated from *Talegalla* (OGILVIE-GRANT, *op. cit.*) as having an almost naked head with a fleshy crest on the crown, a pendulous wattle on the neck, and round rather than oval nostrils. Here again, as in *Eulipoa* and *Megapodius*, the generic differences appear somewhat academic. In any case, these two species are very close in size and appear similar in ecological requirements.

SPECIATION TRENDS

Aepypodius is presumably an old, well-established species complex found in the mountains of New Guinea, as well as a separate, well-marked species on Waigeu, one of the western Papuan Islands. Waigeu is assumed to be very old geologically, pre-Pliocene, termed part of her »Cyclopea» by CHEESMAN (1951). No species of *Talegalla* occurs on Waigeu.

On Misool Island, we found *Aepypodius* for the first time, a new discovery as striking as our finding *Eulipoa*. The species represented is that of the New Guinea mainland, not that of the adjacent island of Waigeu, although there are morphological differences significant enough to warrant the erection of a subspecific category (RIPLEY, 1957). It is assumed that *Aepypodius* has reached Misool from New Guinea during a relatively recent climatic phase, perhaps correlated with a pluvial period, long enough ago to have developed an isolated population which has differentiated at the subspecific level.

Talegalla, which in this case is represented by a monotypic species found in the adjacent west New Guinea lowlands, is considered to be the more recent arrival.

Aepypodius is extremely rare on Misool, had never been recorded by previous collectors, and is only known to the few Arafura hunters who travel widely in the island forests. Its local name is »Gnok». It appears to have a very local distribution in the central limestone hills at about 1,000 feet altitude. The geographical ranges of these species are indicated in Figure 2.

SPECIES COMPETITION

It would appear as if *Aepypodius* and *Talegalla*, closely related as they are, and of nearly identical size with related habits, occurring in a virtually homogeneous environment, were in potential competition on the Island of Misool. Here again, *Talegalla* is the common species on Misool, and *Aepypodius* is extremely rare. In this case, however, we know that *Aepypodius* is apparently confined to the low mountain range (1,000—2,800 feet), although *Talegalla* occurs throughout. The fact that there appears to be a slight range difference here suggests that these hills may represent a marginal habitat for *Talegalla*. MACARTHUR (1958, *op. cit.*) points out that such a dispersal of one species into a more marginal habitat may produce a

Fig. 2. Comparison of the geographical ranges of *Talegalla* and *Aepypodius*. On New Guinea when they occur together, the species are presumed to be altitudinally separated. On Misool *Talegalla* occurs throughout, *Aepypodius* apparently only in the low hills which barely reach 800 meters.

pressure which tends to eliminate a resident species found only in that margina habitat. If this is so, perhaps *Talegalla* is currently exerting potential pressure on the earlier, more narrowly-adapted *Aepypodius* on Misool.

Here again density independent factors presumably enter in. *Aepypodius* on Misool is extremely rare. An instructive example is the related *Aepypodius* species on Waigeu. There, in the absence of *Talegalla*, *Aepypodius* is excessively rare. It had been overlooked or missed by zoological collectors for fifty-three years until its rediscovery in 1938 (DE SCHAUENSEE, 1940). If *Aepypodius* is rare on Waigeu in the absence of competition from *Talegalla*, it may well be that density independent factors are at work on Misool. The obvious one is predation pressure. The mounds of these bush turkeys are well known and under constant surveillance by mammalian, and possibly reptilian, hunters during the egg-laying season. It is assumed that the population has little chance to reach a maximal level in the case of these two large species as in the case of the two smaller ones.

SUMMARY

Four species of megapodes, a peculiar family of galliform birds in which there is no parental care of the young, the eggs being deposited in the ground and hatching independently, are known from the small western Papuan Island of Misool. In the case of the smaller species, *Megapodius* and *Eulipoa*, of approximately equivalent size, no ecological separation is apparent, although elsewhere in the range altitudinal separation occurs.

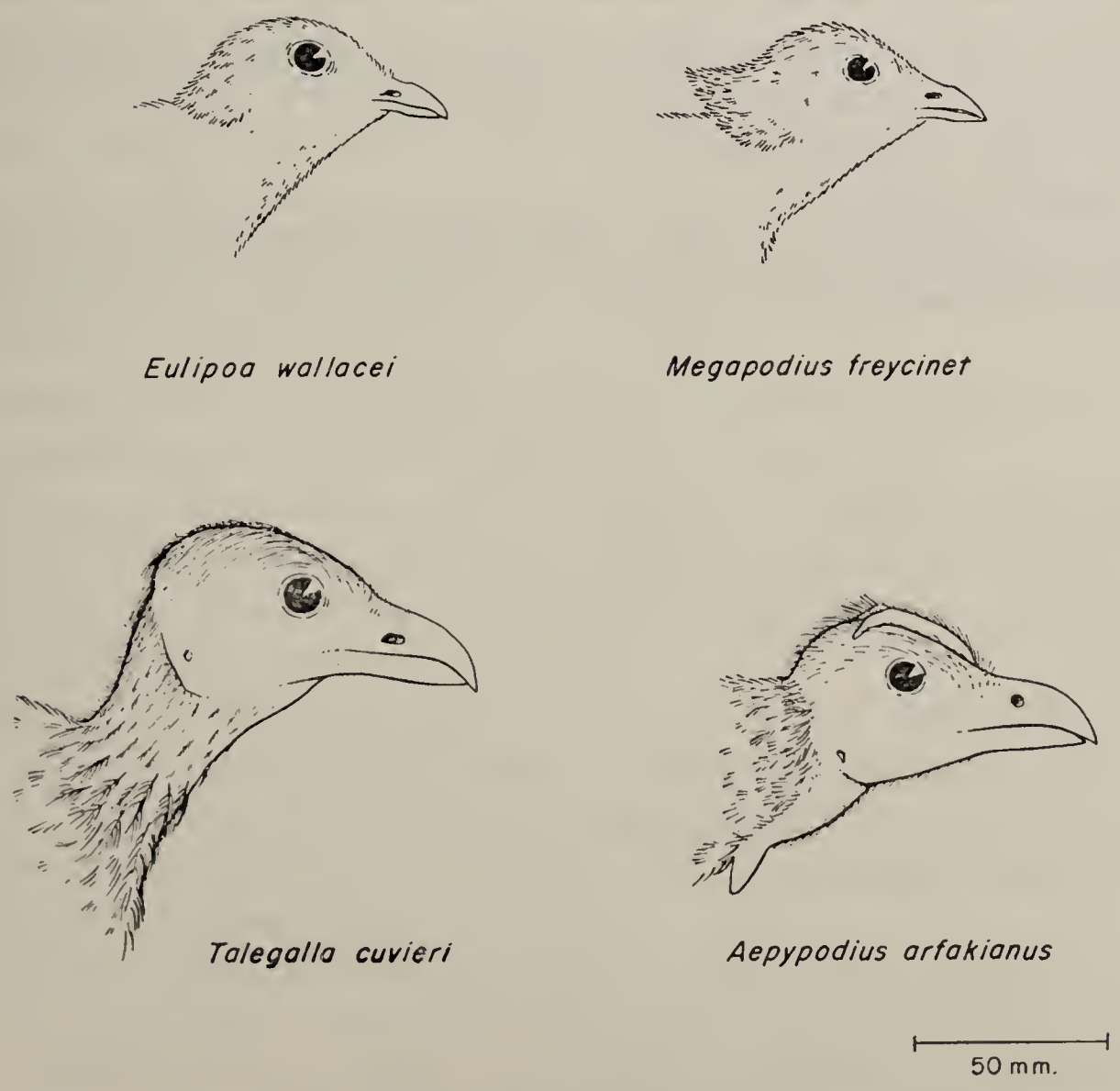

Fig. 3. Comparison of size in the four species.

In the case of the larger species, *Talegalla* and *Aepypodius*, the former invades the marginal habitat of the latter, which has a poorly differentiated range in the central hills of low altitude. Elsewhere in their geographical ranges these species are altitudinally separated, (Figure 3).

If competition can be safely assumed to occur in each instance, only the presence of density independent factors [1], such as predation pressure, can allow these populations to coexist. Presumably the behavior of the species, the lack of parental care of the young, reinforces the effect of predation, thus helping to limit the level of the populations.

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[1] NICHOLSON (1957) prefers the term *non-reactive factor.*

A Tentative Analysis of the Migrational Populations of Starling *(Sturnus vulgaris)*

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In 1938 I pointed out the existence of different migrational populations among Polish Starlings. The present study is a more detailed analysis of this problem based on the results of ringing of Starlings in Poland from 1931 to 1951, with a break during the war years 1939—44. After the war the political frontiers of Poland were changed, in consequence the area studied exceeds in the east the present frontier of Poland and in the west it includes the former German territories.

This study is based on 468 recoveries of Starlings published in the reports of the Ornithological Station in Warsaw, as well as on recoveries published by H. Ecke (1934, 1938) from Silesia, R. Frase (1938) from Grenzmark and W. M. Polivanov (1957) from Bialowieza. All the recoveries have been analysed and all incomplete or doubtful records have been rejected. This leaves records of recoveries of 778 of birds in their first year of life, and 132 of older birds. The material is uniform and refers exclusively to birds native to the area studied.

Two distinct migrational populations can be distinguished among the Starlings of the area studied, one in the north and one in the south.

The wintering grounds of the northern population embrace Holland, Belgium, northern and north-eastern France, and England. From 210 recoveries of birds belonging to this population only 4 were reported from outside the normal wintering grounds, 2 % of the total number of recoveries.

The wintering grounds of the southern population embrace the Dalmatian coast of Yugoslavia, Italy, south-eastern France, south-eastern Spain, Tunisia, Algeria and Morocco. From 272 recoveries of birds belonging to this population only 4 were reported from outside the normal wintering grounds, that is slightly less than 1.5 % of the total number of recoveries.

Between the breeding areas of these populations lies a narrow strip (about 150 kms wide) of mixed area whose birds behave differently from either. They winter not only in the wintering grounds of the main populations but also in the area not used by them, namely south-western France and the remaining part of the Iberian penin-

sula. Their wintering grounds thus include Holland, Belgium, England, France, Italy, the Iberian peninsula, Tunisia and Algeria. This is the most characteristic feature of Starlings breeding in the mixed area. There are breeding localities from which birds wintered in the same year in Belgium, Spain and Italy, thus making use of the whole wintering territory of the species. This feature is found solely in birds coming from the mixed area.

The main populations differ from each other not only in their wintering territories but also in two other biological features, namely the early-summer migration (Frühsommerzug of the German writers), and the number of broods.

In the following discussion the following abbreviations will be used: N for the northern population, S for the southern population, M for the birds of mixed area; and Nw, Sw, and Mw for the wintering grounds of the respective groups.

1. *Winter-quarters.* The winter-quarters of N and S are distinctly separated, embracing completely different areas. The autumn migration of the N birds runs roughly towards WSW, that of the S birds towards SW.

2. *Early-summer migration.* This phenomenon occurs most distinctly among the Starlings of the Baltic countries. But in the area studied only birds of the N population give evidence of it, and even here this phenomenon seems to be not so strongly marked as in birds coming from the more north-easterly breeding grounds. It does not occur at all among the S population.

3. *Number of broods.* Birds of the N population have only one brood, while among the S population two broods annually seem to prevail. This phenomenon has not yet been sufficiently studied either territorially or biologically. The detailed observations in the field should allow a demarcation line between these two categories of birds to be drawn.

4. Summing up the above considerations the following table of differencies could be drawn:

	Population		
	N	M	S
Winter-quarters	NW Europe	NW Europe SW Europe N Africa	SW Europe N Africa
Autumn migration	WSW	WSW SW	SW
Early-summer migration	present	not-present (?)	not-present
Number of broods	one	?	one — two

5. *Problem of the mixed area.* Before we discuss this particular problem some preliminary considerations should be made. A species in a given area may be composed of individual populations which differ from each other in their wintering grounds or migration routes.

An individual population may have:

a. one wintering area which is exclusively occupied by it alone,

b. one wintering area which is shared with another population,

c. several wintering areas.

I propose to call the two first ones (a and b) m o n o h i e m i c populations (the phenomenon as a whole should be called m o n o h i e m y); and the last one (c) p o l y h i e m i c population (p o l y h i e m y).

Salomonsen (1955) introduced some terms referring to a similar problem. He wrote: »In many species the different populations mix freely in the entire wintering ground. Populations which in this way are united in a common winter-quarter I propose to call s y n h i e m i c. Ordinarily the dispersal in winter has been achieved by a spatial division of the available wintering grounds among the different populations. Such populations, which have separate winter-quarters, are called here a l l o h i e m i c. In some species the populations hold an intermediate position between the state of s y n h i e m y and a l l o h i e m y, in other species some populations are synhiemic while others are allohiemic.»

The terms proposed in this paper characterize the individual populations, those introduced by Salomonsen characterize the mutual relations between two or more individual populations. Thus both terminologies supplement each other. Consequently two monohiemic populations may be either allohiemic (different wintering grounds) or synhiemic (common wintering grounds).

The problem of polyhiemic population is more complex. Starlings, for instance, from the Mixed Area may have three different wintering areas: Nw, Sw and their own Mw. They are synhiemic in Nw and Sw (they share these areas with the allohiemic populations N and S) but behave as a monohiemic »population» in their own (exclusive for the moment) wintering area Mw.

Salomonsen's intermediate populations being partly syn- or allohiemic may be considered either as mono- or polyhiemic ones, depending on in which and in how many areas they winter.

The N and the S populations of Starling in the studied area are monohiemic and allohiemic. The polyhiemic birds from the M area have been discussed above.

Polyhiemy is a typical and characteristic feature of M birds. There are a number of localities from which the birds have chosen various combinations of wintering grounds. The localities from which the birds wintered in several areas show quantitively an interesting percentual regularity. Monohiemy in the Nw is shown by birds from about 25 % of localities (precisely 15 from 56), monohiemy in the Sw — 20 % (11 from 56), monohiemy in the Mw — 25 % (15 from 56). Polyhiemy is demonstrated by birds from 25 % of localities. It must be pointed out, however, that birds from 45 % of localities (27 from 56) wintered, partially at least, in the Mw. This shows that this area is favoured by Starlings from the Mixed Area.

The percentual figures stated above demonstrate clearly the intermediate or rather transitional character of the Mixed Area. If the localities were actually situated with equal regularity in the zones shown theoretically by the sequence N — M — S, the matter would be simple and clear. This, however, is not the fact. Actually the

localities from which birds demonstrated the northern or southern monohiemy are distributed irregularly. In this respect the Mixed Area is really a »mixed» one.

The narrowness of the Mixed Area (150 kms) shows its transitional character. One could hardly imagine that a separate population of birds would inhabit a narrow strip of territory without any marked topographical or ecological barriers. On the other hand the sharpness of the boundaries of both populations as shown by the present material arrests one's attention. One would expect a transitional area between two large populations to be wider and its boundaries not so sharply marked.

It is apparent that up to date material from the Mixed Area is too small to allow more general conclusions. The above considerations are, therefore, only a tentative analysis of the phenomenon. Although more results of ringing may considerable change the present picture, it seems that the method applied for analysis is correct and should lead to the correct generalizations.

An important problem for both populations, but especially essential for the Mixed Area, is whether individual birds spend consecutive winter seasons in the same winter-quarters or not. Only birds themselves could answer this important question, but unfortunately repeated retraps of individual birds are very scarce. Up to now we have only one such a case: a bird ringed in October in Salo del Garda, Italy, was trapped and released in Poland in May, and killed next January again in Italy in Bologna.

It would be extremely interesting to ascertain whether polyhiemy occurs not only among birds breeding in the same locality but also among the members of the same family. If we succeed in getting evidence that birds of the same brood wintered in Italy and in Belgium in the same winter, this fact would have great theoretical importance.

Summing up, I think the Mixed Area should be considered a transitional zone between two distinct populations. It shows, however, some strange and peculiar features which could lead to different conclusion. Only more recoveries of ringed Starlings could supply us with material with which to study this problem more precisely.

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Orientation of Nocturnal Bird Migrants by the Stars[1]

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The nocturnal orientation on migration flights was investigated in Garden Warblers *(Sylvia borin)*, Blackcaps *(S. atricapilla)*, Whitethroats *(S. communis)* and Lesser Whitethroats *(S. curruca)*. Ringing results indicate that these small warblers use different migration routes which may have originated during the diluvial glaciation. In the autumn Garden Warblers, Blackcaps and Whitethroats migrate to the S.W. if they come from West Europe, to the S.E. if from East Europe. Birds from the intermediate zone migrate S. It has still to be checked, by breeding experiments, whether genetical differences exist between these populations. All (or nearly all) the Lesser Whitethroats prefer the S.E. route (see Brickenstein-Stockhammer and Drost 1956, *Die Vogelwarte* 18: 197—210). In more southerly latitudes those birds moving S.W. and S.E., change to a S. course.

Garden Warblers leave Europe in August, migrating to winter quarters in Central, West, East and South Africa. The juveniles as a rule leave before the adults. The other species follow in September. Whitethroats winter from the southern edge of the Sahara to South Africa, Blackcaps from southern Europe and North Africa eastwards to Nyasaland and westwards to French Guinea. The Lesser Whitethroats winter in the highlands of Abyssinia and in the Sudan westwards to Lake Chad.

In 1954 we began experiments to determine the sign stimuli or orientation patterns by which these birds were guided on their specific routes on these long distance migrations. During autumn and spring migration warblers were placed in a circular cage. Under the migratory urge the birds fluttered in certain directions, staying on the ring-shaped perch after they had failed to fly out a few times. The cage could be rotated, was about 40 inches in diameter, and had the sides covered with light-proof black felt. The birds could only see a circular section of the sky, subtending about 68°. They could see no external landmarks and any marks on the cage could be prevented from giving directional clues. Experiments under the natural sky were

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[1] Enlarged English Summary. The full paper, with illustrations, is published in *Zeitschrift für Tierpsychologie 14:* 1957, 29—70. The South-West African experiments will be published in *Die Vogelwarte* 1959.

done in autumn 1954 and spring 1955 in Freiburg (48° N, 7°50′ E), and in autumn 1957 and spring 1958 in South West Africa at Okahandja (21°59′ S, 16°56′ E) and Ombu (21°26′ S, 15°20′ E).

Birds belonging to West European populations (the origin of birds captured in South West Africa was uncertain) chose a direction coinciding with the specific seasonal migratory direction. In Freiburg Garden Warblers and Blackcaps headed mainly S.W. in autumn and N.E. in spring. In South West Africa Garden Warblers and Whitethroats faced mainly S. in the autumn and N. in spring. Adequate functioning of this orientation at both places was independent of whether or not the birds had had migratory experience or, indeed, had seen the sky by day or night prior to the experiments. Garden Warblers and Blackcaps which had been reared in isolation from the egg without ever seeing the sky, orientated in the same manner as the other birds, after a short period of hesitation.

Moonlight and bright shooting stars caused alterations in direction. These positive phototactic effects perhaps only occur in the experimental situation, but they do demonstrate an extreme visual sensitivity. When the sky began to cloud up the birds became more and more uncertain of their direction, and with complete heavy overcast they were disorientated and preferred no particular direction. The same result was obtained in control experiments in rooms under diffuse or polarised light. That is, if the light was exactly above the centre of the cage; the slightest eccentricity of the light resulted in positively phototactic responses. The cage itself did not give any directional clues.

All these experiments indicated a possible method of visual orientation. To test this, experiments were started in 1956 under an artificial starry sky, 20 feet in diameter, in the planetarium of the Mariners' School at Bremen (53°6′ N, 8°47′ E). The »North point» of the planetarium had a bearing of 336°. (The planetarium was later moved to a new location 3 ½ miles away and the new »North point» bears 041°.) The effects of parallax, which would produce false results, could be offset. The planetarium sky could not be moved continuously to keep pace with the natural rotation. It was kept in one position during the whole of a short experiment of not more than one hour, or else re-adjusted every 15 minutes.

Under the starless but diffusely illuminated cupola the birds' fluttering was just as disorientated as under heavy cloud or in the indoor control experiments. With the artificial starry sky correctly adjusted to local conditions of time and latitude the birds chose their seasonal migratory directions, relative to the artificial planetarium directions in both locations. The first Blackcap tested in spring 1956 showed a N.E. direction tendency. In autumn 1956 Garden Warblers and Blackcaps preferred a S.W. direction, Lesser Whitethroats preferred S.E. One of the Lesser Whitethroats had been kept in total darkness during its first autumn and spring migratory periods. Now, in the third migration period of its life it was allowed for the first time to see the artificial starry sky. From the first experiment this isolated bird preferred the S.E. planetarium direction.

This same Lesser Whitethroat was examined under a planetarium sky shifted in declination to simulate more southerly latitudes. With declinations from 50° N to 40° N the bird headed mainly S.E. Under 35° N, 25° N and 20° N it gradually shifted its heading from S.E. towards S., while under 15° N and 10° N it faced due S. This bird which had spent its life in a cage and had never travelled under a natural sky displayed the same ability as its wild companions to use the guidance of the stars in the manner appropriate to the species, without previous experience. Adjusting itself to given latitudes, that is to the declination of the artificial starry sky, the bird changed its course from S.E. to S. Within one small planetarium the bird behaved precisely like all Lesser Whitethroats on their way to Africa. Just as the bird in the planetarium, these change their bearings in the region of the Eastern Mediterranean from S.E. to S. We were particularly impressed to observe that under the southerly latitudes, 15° N and 10° N, the bird was weakly motivated to fly; but when the sky was shifted back to 50° N its migratory urge was again very strong. So we may conclude that the azimuth and declination of the star pattern are important for the functioning of this migratory orientation. From the star pattern the bird not only gets the information as to which direction it must fly in, and when to change that direction, but also how far it has to fly.

The effect of false azimuth settings of the starry sky varied and depended on the degree of shifting. The artificial sky adjusted to a different time presents an ambiguous situation to an observer with a good clock or sense of time. At a fixed geographical position the shift might be interpreted as corresponding to a time difference within the 24 hour cycle or to a time difference in the year's cycle. Alternatively the difference might be interpreted as a displacement East (when the sky is shifted to a future time) or to the West (shifted to past time). The interpretation given by a warbler on a false azimuth setting can be determined from its resulting behaviour.

One night we placed the Lesser Whitethroat under a sky 5 h. 10 m. in advance of Local Time. What would the bird do? Would it feel that its inner clock should be shifted forward 5 h. 10 m., that it had overslept and forgotten to start its migratory flight earlier in the night? Then it should still go to the S.E. Would the bird feel that the season had shifted 77 ½ days forward, because the star pattern as presented would at that season be appropriate to the actual Local Time? The bird would then »think» that the migratory period was over and either go back to sleep or hasten to reach its winter quarters, again by flying S.E. In fact, the bird did not interpret the situation in any of these ways. It apparently felt that it had been displaced eastwards by 77°30′, without any alteration of its inner clock. It fluttered furiously, facing West. The obvious desire of the bird to fly back to its starting point was confirmed by another experiment in which the sky was shifted forwards 3 h. 26 m. Again the bird faced West. Only with a shift as small as 1 h. 41 m. did the bird show any deviation from West, facing to the W.S.W. When the time difference was reduced to 1 h. 10 m. the deviation from West was still greater, and had reached S.S.W. by the end of the experimental period. When the sky was only 1 h. earlier than local

conditions the bird started to the South and had turned S.E. as the time difference became zero; thereafter the bird preferred the usual S.E. direction of its autumn migration.

We expected similar responses, but orientated to the East, when we presented the bird with the sky pattern shifted backwards in time. But this bird behaved as if it had not been displaced, and faced S.E. It is likely that its inner clock had been influenced by the previous experiments. We did get the expected eastward compensation under a retarded sky with other birds not previously treated in this way.

When the time differences exceeded six hours the birds showed entirely different reactions which may be briefly summarised. When the star pattern was one that would occur at the experimental point during the night only in summer or winter the birds were disorientated and headed towards all directions. It is likely that they could not see under these sections of the starry sky any of the orientation patterns to which they could have reacted during autumn migration. But if the sky was shifted to positions which would occur during the night in spring, then the birds appeared to be in a quandary whether to face in the autumn or the spring migration direction. In fact they alternated between these directions, changing direction on the average 150 times in half an hour. A Garden Warbler and a Blackcap which were kept for fourteen nights under a »spring» sky during the autumn migration in 1958 did not resolve this conflict in the whole of that time. It is clear that the birds did recognise the star pattern appropriate to the complementary migration period and that this produced a conflict situation.

These planetarium experiments demonstrate that Garden Warblers, Blackcaps and Lesser Whitethroats possess a mechanism for nocturnal migration orientation. This enables them, together with their ability to assess time, to determine their specific migration courses from the starlit sky. Local topography and individual experience are acquired independently. For the functioning of this mechanism it is only necessary for the birds to see a part of the starry sky.

It is important to point out that these birds do not have to rely solely on the constellations. In the daytime they can guide themselves by the position of the sun, as shown by U. v. St. Paul *(Behaviour* 6, 1953, 1—7). On cloudy nights on migration they may get some help from landmarks acting as leading lines helping them out of their orientation difficulties. But when in total darkness they are overtaken by a heavy cloudbank they begin to circle helplessly and are often drawn to lighthouses or else they land. Strong winds can drift the birds in the wrong direction, miles off course. They then have to navigate back to their route when good flight conditions return.

So navigation by the stars is the important key to the long distance orientation of these warblers on their nocturnal migration flights. The hereditary structure of this mechanism is most remarkable. Azimuth and declination of the star pattern are the co-ordinates needed for the functioning of both orientation and goal-directed flights on migration to the winter grounds and breeding quarters.

Ornithosis

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For the first time, a limited epidemic of this severe disease was described by Ritter in Switzerland in 1880. The ornithosis or psittacosis is a disease which is common in birds but rare in man. In the medical literature this disease was first named Psittacosis as it then seemed that only parrots and parakeets were affected. Later, it was also discovered in various other types of birds, and for this reason the designation ornithosis was substituted for the former psittacosis or parrotfever.

This infection not only affects parrot and parakeet families. It was recently shown that many types of birds could be infected. The natural host spectrum for ornithosis is much broader than was thought in earlier times. Over 70 avian species, of which 30 species belong to the parrot family, including Domestic Fowl, pigeons, chickens and Turkeys, can be spontaneous hosts. The virus was found in rice-birds, canaries, and finches. Spontaneous infections are possible in Fulmars, petrels, Herring-gulls, Willets, and other birds.

Ornithosis is caused by a virus belonging to the pneumonitis, psittacosis, lympho-granuloma-venereum group of disease agents. Clinically speaking, it is a very different disease. The virus in question, a highly toxic agent, is necessarily intra-cellular like the rickettsia. All these viruses are of large size. Psittacosis and lympho-granuloma showed large elementary bodies. In experimental studies several animals are used for laboratory tests e.g. White Mice, Rabbits, Hamsters, Cotton Rats, Rhesus Monkeys. For routine examination the White Mouse is most frequently used. Cultivation of this virus in the chicken embryo is not difficult and the inoculation into the yolk of an egg is easy. 3—7 days after an oculation the embryo dies. The post mortem examination of these embryos reveals a general spreading of the virus in all organs.

It is an important fact that many birds can be hosts of psittacosis virus. The brood can be infected in the nest by the parent-birds secreting the virus. It appears that young birds never show a severe form of this disease. But this process of infection is subject to a sudden change now and again. It is known, that in excrements and secretions the number of virus varies a great deal. A concomitant illness can be responsible for this fact.

The discovery that the infection in man is caused not only by birds of the parrot and parakeet groups but also by Domestic Fowl, is an important one. This illness is very dangerous and unpredictable, if not uncanny.

An infection in birds or in man is possible at any time. Birds, mammals, and the human being may become host of this virus.

The pathological-anatomical findings in ornithosis are very varied. Birds often show an exanthema. A further characteristic is the severe mucoid or fibrinous exudation in the air sacs. The spleen, the liver, the kidneys, and the muscles are organs showing a high number of virus. All birds affected show an exudation in the pericardial and peritoneal cavity. In this exudation the number of virus is very high. Various organs and membranes show haemorrhagies. The pathological-anatomical findings in man differ from those in birds. In man a severe form of atypical pneumonia without reaction on the pleura and with leucopenia can be found. The process is an acute one with high temperature and a high mortality rate. In the beginning patients complained about headaches. In mammals we found a more severe inflammation in the interstitial tissue. The cells lining the alveoli are in proliferation. They show frequent mitosis, lying free in the lumen of the alveoli, mixed with mononuclear cells and few neutrophile elements. In the alveoli a gelatinous exudation with red blood cells can also be found. In some organs, especially the liver, kidney, and spleen, there are small necroses. Lymphnodes and spleen are enlarged and in a softening condition. In birds we can observe an explosive epidemic phase or a stabilised, symptomfree endemic state.

It seems that the influences of weather and temperature are of importance for the outbreak of the disease especially with birds in captivity.

Human infections in 1952—1954 in the United States: Texas, New Jersey, California and Oregon indicated that Turkey ornithosis was the source. Ornithosis agents could be isolated from infected Turkeys.

An infection with ornithosis in Domestic Fowls can be much more dangerous to the human being. Any person handling infected birds and objects can fall ill.

The importance of ornithosis as a disease is often underrated. It is not, as is commonly believed, only a rare infection of some groups of birds.

Ringfundmeldungen lassen Schleifenzug bei der mitteleuropäischen Wachtel, *Coturnix coturnix*, vermuten

Alfred Schifferli

Schweiz. Vogelwarte, Sempach

Nach unsern Erkundigungen bei andern Beringungszentralen fehlen bis jetzt Fernfunde von Wachteln, die in ihrem mitteleuropäischen Brutgebiet beringt wurden. Die wenigen Funde beringter Wachteln in der Schweiz gewinnen deshalb an Bedeutung. Sie sollen hier, in Verbindung mit den zahlreichen Ringfunden von Wachteln, die in Italien während des Frühlingszuges gefangen wurden, verglichen werden. Wie die nachfolgenden Ausführungen zeigen, ergänzen sie sich und führen zu denselben Schlussfolgerungen. Damit erhalten wir wenigstens in groben Zügen ein Bild des Wachtelzuges.

MATERIAL

Jeden Sommer werden in der Schweiz beim Grasmähen und während der Getreide-Ernte zahlreiche Wachtelnester zerstört. Es gelang Mitarbeitern und uns, rechtzeitig in den Besitz solcher verlassener Wachteleiern zu kommen. Sie wurden im elektrischen Apparat künstlich ausgebrütet und die Kücken grossgezogen. Im Alter von 4—6 Wochen wurden sie beringt freigelassen, seit 1945 insgesamt 169 Jungwachteln. Weitere 130 Wachteln unbestimmten Alters wurden meist während der Herbstzugzeit zufällig gegriffen und beringt freigelassen.

Die italienischen Jäger benützen lebende Wachteln zum Abrichten ihrer Hühnerhunde. Zu diesem Zwecke wird der sonst während der Frühlingszeit verbotene Wachtelfang unter staatlicher Kontrolle gestattet. Die Wachteln werden meist im untern und mittleren Teil der adriatischen Küste und auf den Pontinischen Inseln im April und Mai gefangen und zur Hauptsache Jagdgesellschaften im Raume von Genua-Turin bis zur Po-Ebene abgegeben. Bei der Arbeit mit dem Hund wird die Wachtel voll flugfähig freigelassen. Sie soll anschliessend von ihm gesucht und vorgestanden werden ohne ihr weiteres Fortkommen zu beeinträchtigen. Prof. Dr. A. Toschi, Lab. di Zool. applicata alla Caccia, Bologna hat diese Dressur-Methode der Beringung dienstbar gemacht. So wurden in den Jahren 1938—54 insgesamt um 500,000 Wachteln beringt. Dabei handelt es sich fast ausnahmslos um ♂♂, die vom Fänger mit dem Ruf des ♀ unter die gestellten Netze gelockt und dann gefangen wurden. Mehr als 6,000 Ringfunde wurden gemeldet. Sie beweisen die Brauchbarkeit dieser Methode.

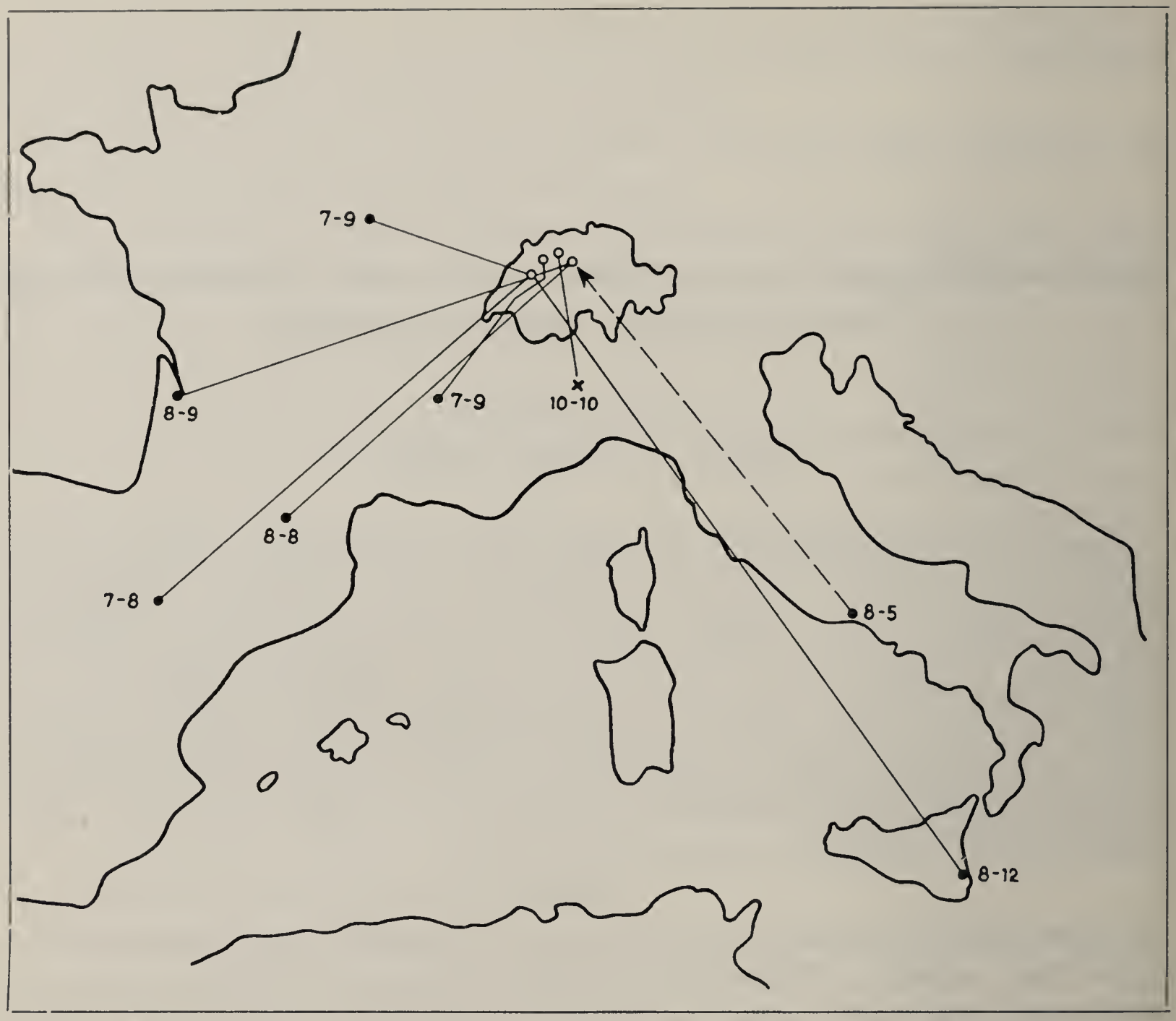

Abb. 1. Ringfunde in der Schweiz beringter Wachteln ○ = Beringungsort, ● = Fundort jung beringter Wachteln, *x* = Fundort einer im Herbst gefangener Wachtel unbestimmten Alters, Ziffern = Beringungs- und Fundmonat (alle im selben Lebensjahr).

ERGEBNISSE

Der Wegzug im Herbst führt die in der Schweiz beheimateten Wachteln in südwestlicher bis westlicher Richtung nach Frankreich und Spanien. Der Dezemberfund aus Sizilien macht es wahrscheinlich, dass ausnahmsweise Wachteln aus der Schweiz den Weg über Italien ins Winterquartier wählen. Eine bei Aarau im Oktober gefangene Wachtel wurde im selben Monat bei Turin erlegt. Ob sie über Italien oder Frankreich weitergezogen wäre, bleibt ungewiss. — Die Rückkehr im Frühling — siehe Maifund bei Rom — führt über Italien, was dann mit aller Deutlichkeit aus Abb. 2 hervorgeht.

Zu diesen Funden aus der Brutzeit (Abb. 2) kommen noch weitere 30 Funde aus den Monaten August—September, die wenigstens zum Teil ebenfalls in der Schweiz brütende Wachteln betreffen. Auf Grund dieser Ergebnisse steht fest, dass die Wachteln im Frühjahr über Italien die nördlich und nordöstlich der Alpen gelegenen

Abb. 2. Schweizerische Wiederfunde in Italien beringter Wachteln ○ = Beringungsort (April—Mai), ● = Fundort (Mai—Juli).

Brutgebiete anfliegen. Der Zug über die Alpen aus südlicher Richtung muss ganz erheblich sein, im Gegensatz zum Herbstzug.

Zum bessern Verständnis der Abb. 3 müssen wir vorausschicken, dass im Frühling durch Italien ziehende Wachteln im Raume nördlich und nordöstlich der Alpen (vom Rhein bis nach Polen) brüten, was auf Grund von zahlreichen Ringfunden hervorgeht (Toschi 1956). Die hier eingezeichneten Herbstfunde rühren von Wachteln dieser Brutgebiete her. Die Funde schweizerischer Jungwachteln liegen im selben Raum. Es fällt die starke Häufung am Westrand der französichen Alpen auf. Der Weiterzug geht über Spanien nach Nordafrika. Auf direkten Zug über das westliche Mittelmeer weisen die Funde auf den Balearen hin. Marokko scheint mehr als Durchzugsland und weniger als Überwinterungsquartier benutzt zu werden, fehlen doch

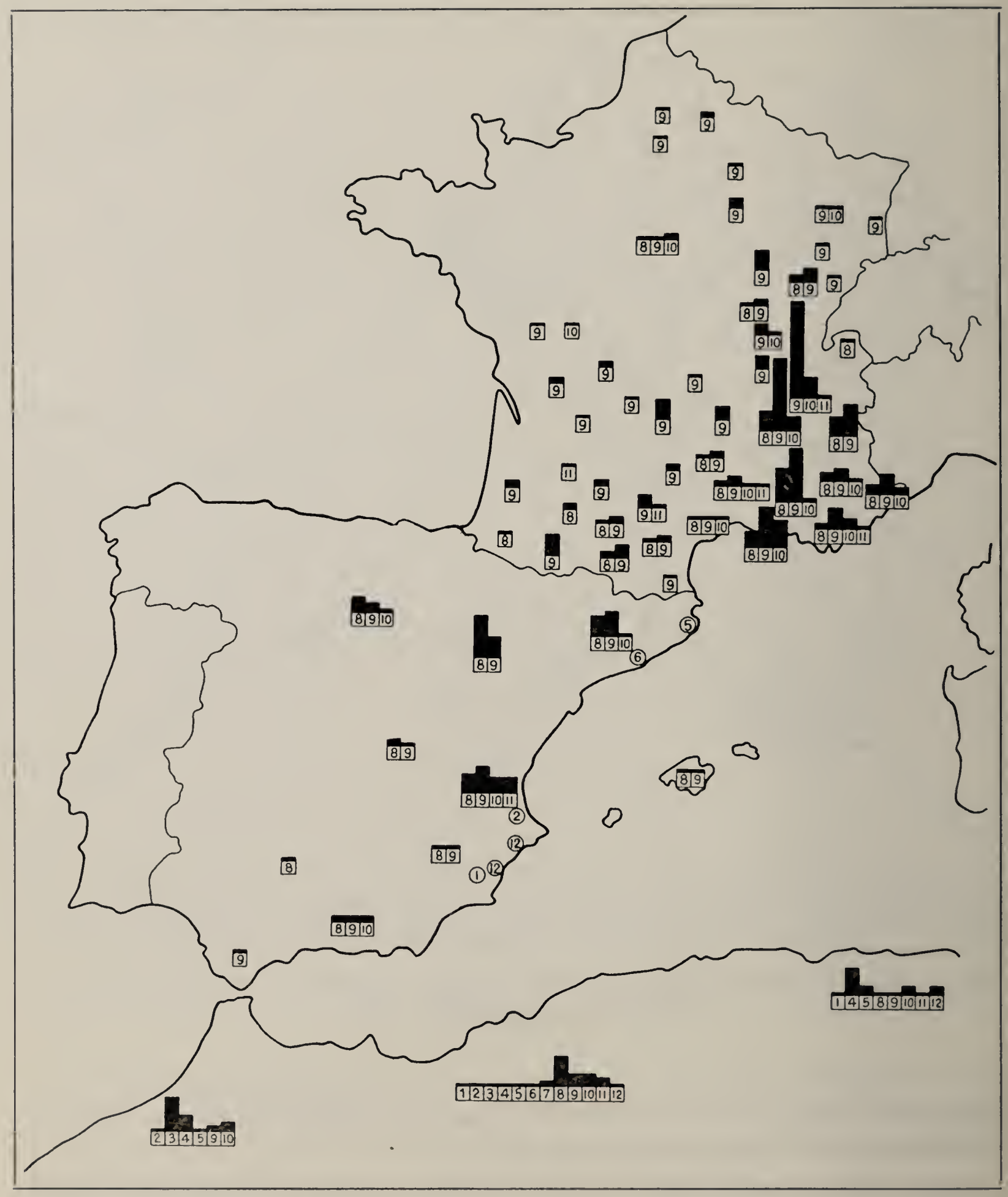

Abb. 3. In Italien beringte Wachteln, Herbstfunde nord- bis süd-westlich der Alpen (nach TOSCHI 1956). Säulen = monatsweise Zusammenfassung der Funde für die Departemente für Frankreich und Nordafrika und die spanischen Provinzen. Niedrigste Säule = 1 Fund. Ziffern = Fundmonate.

Funde aus den eigentlichen Wintermonaten. Zwei weitere Funde, einer von Casablanca, der andere aus dem Senegal (siehe Abb. 4) zeigen südwärts gerichteten Weiterflug. In Algier dagegen werden in jedem Monat Wachteln mit italienischen Ringen angetroffen, Häufung zur Herbstzugzeit. In Tunesien finden wir die Wachteln vor

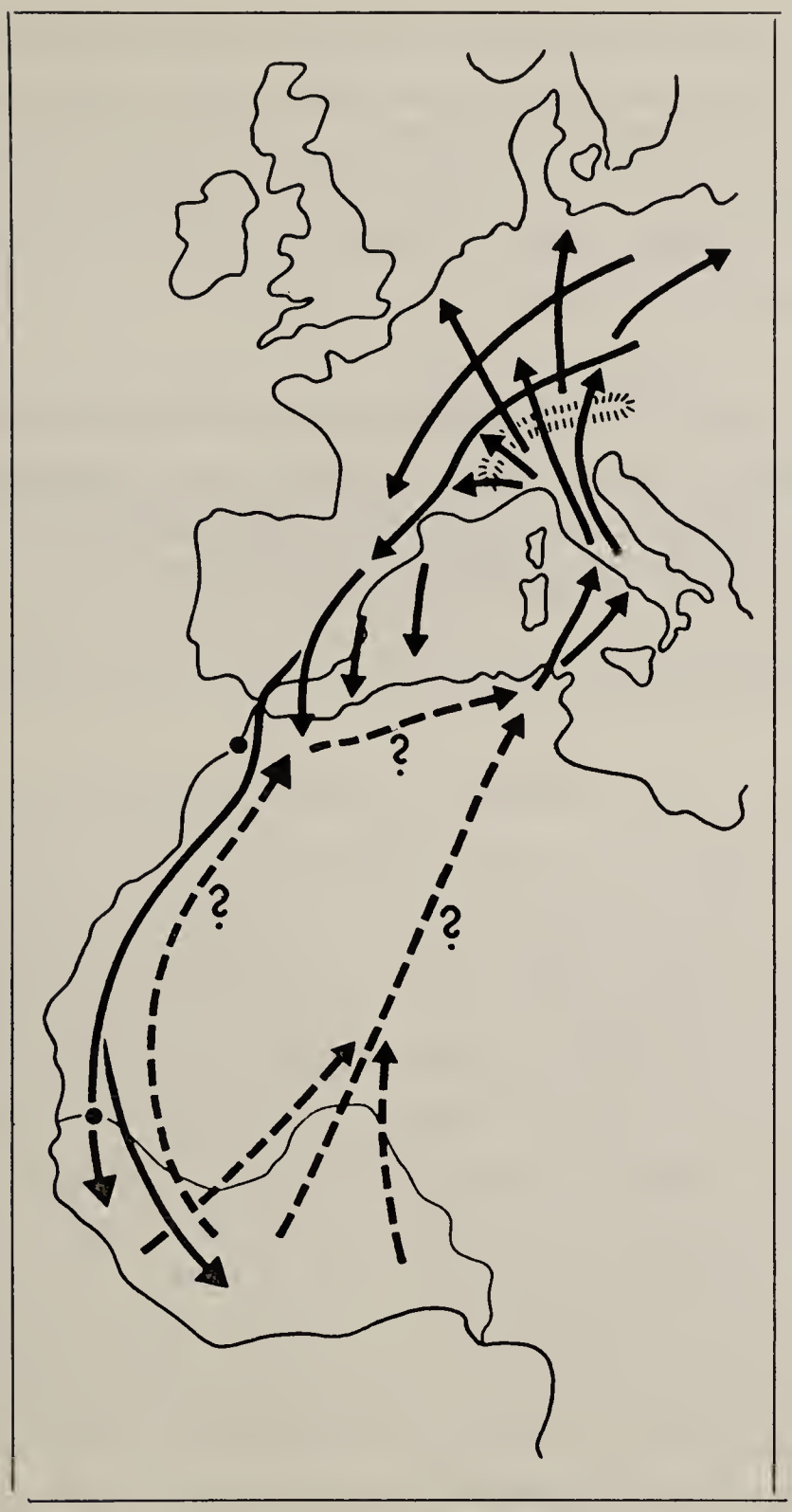

Abb. 4. Zugwege der mitteleuropäischen Wachtel auf Grund der Beringung. Linien und Pfeile zeigen Zugrichtung im Herbst und Frühling, die gebrochene Linien die hypothetischen Möglichkeiten der Zugschleife. Die Punkte beziehen sich auf die Funde italienischer Wachteln von Casablanca und dem Senegal.

allem zur Frühjahrszugzeit. Wenige Wachteln überwintern bereits in Spanien (Dezember/Februar-Funde). Dagegen fehlen Funde aus Spanien zur Frühjahrszugzeit (März/April), abgesehen von einem einzigen Maifund. Damit wird die Bedeutung Italiens als Durchzugsland im Frühjahr für die nördlichen und nordöstlichen europäischen Brutpopulationen noch offensichtlicher.

Nach Ringfunden und Beobachtungen erfolgt der Abflug der Wachteln aus Nordafrika im Gebiet des tunesischen Golfes (Cap Blanc), von wo aus diese Vögel im nächtlichen Fluge die italienische Küste zwischen Neapel und Rom ansteuern. Aus der Tatsache, dass der Herbstzug über Spanien, der Frühjahrszug aber über Italien führt, werden die in Nordafrika überwinternden Wachteln in östlicher Richtung Tunesien

zufliegen müssen. Dasselbe gilt für die im Senegal- und Kongogebiet überwinternden Wachteln, die zur Erreichung dieses Zwischenzieles eine mehr nordöstliche Richtung einzuschlagen haben. Wie diese, den Herbstzug mit dem Frühjahrszug verbindende Zugschleife zustande kommt, und welches die dazu notwendigen Ursachen sind (erblich festgelegter Zugweg, äussere Faktoren wie z. B. Windeinfluss?), darüber wissen wir vorläufig noch nichts.

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Über die Hemmung der Mauser auslösenden Wirkung des Thyroxins durch Testosteronpropionat beim Grünfinken, *Chloris chloris* (L.)

H. Schildmacher

Vogelwarte Hiddensee, Deutsche Demokratische Republik

Allgemein wird angenommen, dass die Schilddrüse eine wesentliche Rolle bei der Auslösung der Mauser spielt. Künstliche Zufuhr von Schilddrüsensubstanz oder Thyroxin, peroral oder per injectionem, löste bei ausreichender Dosierung bei allen untersuchten Vogelarten zu beliebiger Jahreszeit eine Mauser aus, wobei allerdings einschränkend gesagt werden muss, dass die bekanntgewordenen Versuche zum überwiegenden Teile an körnerfressenden Vögeln durchgeführt wurden. In eigenen, nicht veröffentlichten Untersuchungen gelang jedoch Auslösung der Mauser auch beim Star (*Sturnus vulgaris* L.) und Rotkehlchen (*Erithacus rubecula* (L.)). Soweit die Schilddrüsen von Vögeln, die sich am Beginn der Mauser befanden, histologisch untersucht wurden, zeigten sie starke Aktivität. Wir fanden dies u. a. bestätigt beim Grünfinken (*Chloris chloris* (L.)) und der Sturmmöwe (*Larus canus* L.). Beim Gartenrotschwanz (*Phoenicurus phoenicurus* (L.)) konnte gezeigt werden (Schildmacher 1952), dass zur Zeit des Mauserbeginns der Ruheumsatz um 44.2 % erhöht war, was ebenfalls als Zeichen einer starken Ausschüttung von Schilddrüsenhormon zu werten ist.

Nun finden wir aber eine stärkere Ausschüttung der Schilddrüse auch zur Zeit der Gonadaktivität (Schildmacher 1956), jedoch wird zu dieser Zeit keine Mauser beobachtet. Nehmen wir also, wozu wir aufgrund aller bisherigen Beobachtungen berechtigt sind, an, dass die Mauser durch eine Ausschüttung von Schilddrüsenhormon ausgelöst wird, so müssen wir vermuten, dass die gleichzeitige Anwesenheit einer aktiven Keimdrüse bezw. grösserer Mengen von Keimdrüsenhormon die Mauserauslösung durch Schilddrüsenhormon hemmt oder verhindert.

Streich u. Svetosarov (1936, 1937, 1938) geben an, dass kastrierte Vögel dauernd mauserten. Ähnliche Angaben macht Dorothea Starbuck Miller (1939) für Sperlinge (*Passer domesticus* (L.)). Benoit u. Aron (1931) fanden bei Huhn und Ente nach Kastration im Frühjahr eine Zunahme an TSH. Schliesslich beobachtete Rautenberg (1952/53), dass kastrierte Grünfinken (*Chloris chloris* (L.)) im künstlichen Langtag im Frühjahr mauserten und sehr aktive Schilddrüsen besassen,

während kastrierte Vögel derselben Art in der normalen kurzen Tagesdauer des Januar und Februar Speicherschilddrüsen besassen und nicht mauserten.

An anderer Stelle (SCHILDMACHER 1956) wurde schon berichtet, dass männliche und weibliche Grünfinken, die als Kontrolltiere Implantate von Paraffin in die Schlüsselbeingrube erhalten hatten, zum Teil abnorme Mauser zeigten, dass ferner 18 von insgesamt 22 männlichen Grünfinken, die Depots von Dienäthylstilboestrol trugen, zu verschiedenen Jahreszeiten abnorme Mauser zeigten, während von 9 Weibchen der gleichen Art, die ebensolche Depots von Dienäthylstilboestrol erhalten hatten, keines mauserte. Es entstand dabei der Eindruck, dass das eigene Keimdrüsenhormon die von den übrigen Faktoren auszulösende Mauser verhinderte. Indessen konnten diese Beobachtungen noch nicht als beweisend angesehen werden, so dass wir bis jetzt noch nicht weiter gelangt waren als WOITKEWITSCH u. NOWIKOW (1936), die schon damals eine Korrelation zwischen Gonadaktivität und Mauser

TABELLE 1

Männliche und weibliche Grünfinken mit und ohne Depots von Testosteronpropionat, im Januar, bei inaktiver Gonade unter dem Einfluss intramuskulärer Injektionen von Thyroxin

T = 0.25 mg Thyroxin; t = 0.2 mg Thyroxin;
m = Mauser; — = nicht injiziert, keine Mauser.

♂♂		♀♀	
Nr.	*Mit Depot*	Nr.	*Mit Depot*
61	TT - tttmm	81	TT - t - - - - - - - - - - -
59	TT - tttmm	85	TT - t - - - - - - - - - - -
52	TT - ttt - mmmmmmmmmm	78	TT - ttt - - - - - - - - - -
58	TT - ttt - mmmmmmmmmm	77	TT - ttt - - - - - - - - - -
53	TT - ttt - m	75	TT - ttt - - - - - - - mmm
51	TT - ttt - - mmmmmmmmm	79	TT - ttt - - - -mmmmmmm
57	TT - ttt - - - mmmmmmmm		
54	TT - ttt - - - - - - - - - -		
62	TT - ttt - - - - - - - - - -		
56	TT - tt - - - - - - - - - - -		
55	TT - t - - - - - - - - - - - -		
	Ohne Depot		*Ohne Depot*
74	TT - ttt - mmmmmmmmmm	91	TT - ttt - mmmmmmmmmm
66	TT - tttmmmmmmmmmmm	92	TT - t - - mmmmmmmmmmm
67	TT - tttmmmmmmmmmmm	87	TT - tt - mmmmmmmmmmm
70	TT - tttmmmmmmmmmmm	89	TT - tttmmmmmmmmmmm
71	TT - tttmmmmmmmmmmm	93	TT - tttmmmmmmmmmmm
72	TT - tttmmmmmmmmmm	97	TT - tttmmmmmmmmmm
73	TT - tttmmmmmmmmmmm	88	TT - ttmmmmmmmmmmmm
63	TT - ttmmmmmmmmmmmm	90	TT - ttmmmmmmmmmmmm
65	TT - ttmmmmmmmmmmmm	94	TT - ttmmmmmmmmmmmm
69	TT - ttmmmmmmmmmmmm	95	TT - ttmmmmmmmmmmm
		96	TT - ttmmmmmmmmmmm
		98	TT - ttmmmmmmmmmmm

vermuteten, zugleich aber betonten, dass der Beweis einer Kausalität noch ausstehe.

Gemeinsam mit meinem Mitarbeiter Dr. RAUTENBERG unternahm ich nun neuerdings den Versuch, am Grünfinken nachzuprüfen, ob in der Tat Keimdrüsenhormon einen Einfluss auf die Auslösung der Mauser durch Thyroxin habe.

Wir versahen eine Anzahl männlicher und weiblicher Grünfinken mit Depots von je 16—24 mg Testosteronpropionat, die in die Schlüsselbeingrube gesetzt wurden. 20 Tage später begannen wir, diese Tiere mit täglichen intramuskulären Injektionen von Thyroxin zu behandeln. An den ersten beiden Tagen betrug die Tagesdosis 0.25 mg. Wegen des starken Gewichtsabfalles unterliessen wir am dritten Tage die Injektionen und gaben dann vom vierten bis zum sechsten Tage 0.2 mg pro die. Der gleichen Behandlung mit Thyroxin unterwarfen wir zur gleichen Zeit (im Januar) eine Anzahl männlicher und weiblicher Grünfinken ohne Depots von Testosteronpropionat, deren Gonaden sich, wie Stichproben zeigten, zu dieser Zeit im Ruhezustande befanden. Tabelle 1. zeigt das Ergebnis:

Abb. 1—4. Links oben: Maximale Mauser eines Grünfinken ohne Depot von Testosteron.
Rechts oben: Minimale Mauser eines Grünfinken ohne Depot von Testosteron.
Links unten: Maximale Mauser eines männlichen Grünfinken mit Depot von Testosteron.
Rechts unten Maximale Mauser eines weiblichen Grünfinken mit Depot von Testosteron.

Es ist deutlich zu sehen, dass bei den Kontrollen die Mauser am 6. bezw. 7. Tag der Thyroxinbehandlung einsetzte. Nur in zwei Fällen begann sie erst am 8. Tage. Bei den Weibchen mit Depot trat überhaupt nur in 2 Fällen Mauser ein, und zwar erst am 11. bezw. 14 Behandlungstag. Bei den Männchen mit Depot blieb in 4 Fällen die Mauser aus, nur in 2 Fällen setzte sie am 7. Tag ein (bei einem dieser beiden Tiere wurde bei der Sektion kein Depot mehr gefunden!), in den übrigen Fällen erst am 8. Tag bezw. später. In beiden Geschlechtern hatten also die Depots von Testosteronpropionat die Mauser verzögert bezw. verhindert, die bei den Kontrollen ohne solche Depots prompt eingetreten war. Dazu ist noch zu ergänzen, dass auch die Intensität der Mauser durch die Depots abgeschwächt war: Während die Vögel ohne Depot das gesamte Gefieder verloren, allenfalls mit Ausnahme der Handschwingen und weniger Decken (Abb. 2. zeigt den Kontrollvogel mit der geringsten Mauserintensität dieser Gruppe), beschränkten sich die Federverluste bei den Depotvögeln auf den grössten Teil des Kleingefieders, einen Teil der Schwanzfedern und allenfalls einzelne Armschwingen. (Abb. 3. und 4. zeigen die Depotvögel mit der grössten Mauserintensität in dieser Gruppe.)

Es könnte gegen diese Ergebnisse immerhin der Einwand erhoben werden, dass die Depots mehr Testosteron an den Kreislauf abgeben, als aktive Keimdrüsen. Aus diesem Grunde führten wir das *experimentum crucis* durch: Eine Anzahl männlicher Grünfinken wurde im Februar kastriert und dann im Mai zusammen mit normalen Männchen, deren Keimdrüsen, wie Stichproben ergaben, zu dieser Zeit voll aktiv waren, mit Thyroxin behandelt. Dabei erhielt je ein Teil beider Gruppen an

TABELLE 2

Männliche Grünfinken, kastriert bezw. mit aktiven Testes im Mai, unter dem Einfluss intramuskulärer Zufuhr von Thyroxin

t = 0.2 mg Thyroxin; m = Mauser; -- = keine Injektion und keine Mauser.

Nr.	*Kastraten*	Nr.	*Kastraten*
20	ttttttmmmm	18	tt - t - t - mm
21	tttttmmmmm	03	tt - t - tmmmm
07	tttttmmmmm	06	tt - t - tmmmm
02	tttttmmmmm	09	tt - t - t - - m
15	tttttmmmmm	13	tt - t - mmmmm
14	tttttmmmmm	16	tt - t - mmmmm
01	tttttmmmmm	20	tt - t - mmmmm
05	tttttmmmmm	22	tt - tmmmmmm
19	tttttmmmmm		
	Testes aktiv		*Testes aktiv*
28	ttttmmmmm	33	tt - t - tmmmm
30	tttttmmmm	31	tt - t - t - mm
32	tttttmmmm	35	tt - t - t - mm
34	tttttmmmm	29	tt - t - t - - m
36	tttttmmmm	37	tt - t - t - - m
38	tttttmmmm	39	tt - t - t - - m

6 aufeinanderfolgenden Tagen täglich 0.2 mg Thyroxin intramuskulär, bei den restlichen Vögeln beider Gruppen erfolgte die Injektion nur am 1., 2., 4. und 6. Tage. Tabelle 2. zeigt das Ergebnis:

Bei den täglich injizierten Vögeln begann — mit je einer Ausnahme bei den Kastraten und Kontrollen — die Mauser bei den Kastraten einen Tag früher als bei den geschlechtsaktiven Tieren. Bei den nur an 4 Tagen injizierten Vögeln ist das Ergebnis noch deutlicher: die früheste Mauser eines geschlechtsaktiven Tieres begann am 7. Tage, in 2 Fällen setzte sie am 8. und in 3 Fällen am 9. Tage ein, während bei den Kastraten der Mauserbeginn in einem Falle auf den 5., in 3 Fällen auf den 6., in 2 Fällen auf den 7. Tag fiel und nur in zwei Fällen auf den 8. bezw. 9. Tag.

In 5 Fällen wurden bei der Sektion der Kastraten kleine Hodenregenerate gefunden, jedoch waren diese noch zu klein, um durch ihre Hormonproduktion einen merklichen Einfluss ausüben zu können. Das grösste hatte ein Volumen von 25.7 mm^3, während das kleinste Volumen beider Hoden bei einem Kontrolltier 193.4 mm^3, das grösste 443.5 mm^3 betrug.

Die Ergebnisse der Versuche können also nur so gedeutet werden, dass die Hormonproduktion der aktiven männlichen Keimdrüse bezw. die Hormonabgabe eines Depots von Testosteronpropionat die Induktion einer Mauser durch Thyroxin verhindert oder zumindest hemmt. Es kann daraus weiter gefolgert werden, dass zur Zeit der Geschlechtsaktivität die Anwesenheit des Keimdrüsenhormons die Auslösung einer Mauser durch die zu dieser Zeit aktive Schilddrüse verhindert.

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Zur Frage des Brutreifealters südwestdeutscher Weiss-Störche *(C. ciconia)*

W. Schnetter und G. Zink

Vogelwarte Radolfzell

Die Kontrolle beringter Altstörche durch Ablesen der Ringnummer am lebenden Vogel mit Hilfe von Fernrohren ist, ähnlich wie die Farbberingung bei anderen Vogelarten, zu einem wichtigen Hilfsmittel der Populationsforschung geworden. Solche Untersuchungen wurden mit besonderen »Ableseringen» in Ostpreussen begonnen (Hornberger 1943, Schüz 1952). Mit verfeinerter Methodik werden sie jetzt in ganz SW-Deutschland fortgeführt. In den Jahren 1955 bis 1958 konnten in den Storchbrutgebieten Südbadens (Oberrheingebiet, Hegau und Baar) 55 »Ablesestörche» erfasst werden, eine ganze Reihe davon mehrere Jahre hintereinander. Die Kontrolle aller Störche mit Nestbindung wurde von Jahr zu Jahr auf ein grösseres Gebiet ausgedehnt, 1958 auf ganz Baden und auf grosse Teile der angrenzenden Brutgebiete. Damit kann mit zunehmender Sicherheit das Jahr angegeben werden, in dem Ringstörche erstmals zur Brut schreiten. Für 31 der oben genannten 55 südbadischen Ringstörche ist das Erstbrutalter mit genügender Sicherheit bekannt. Gewertet werden dabei nur die Fälle, in denen — als Beweis für die physiologische Reife — Junge geschlüpft sind. 15 dreijährigen Erstbrütern stehen 7 vierjährige, 5 fünfjährige und ein sechsjähriger Erstbrüter gegenüber. Von drei Störchen, die schon zweijährig zur Brut schritten, wird weiter unten noch die Rede sein. Einer der Vierjährigen war schon dreijährig am gleichen Nest und hat dort möglicherweise bei einem Sturm, der das Nest teilweise zerstörte, das Gelege verloren. Alle anderen Vier- bis Sechsjährigen waren Neuansiedler. Drei der Fünfjährigen und der Sechsjährige waren vierjährig ohne Brut an einem anderen Ort. Der Letztgenannte fehlte in dem Zwischenjahr, war aber fünfjährig mit Sicherheit nirgends in der Umgebung seines späteren Brutorts als Brutvogel.

Man darf natürlich nicht »Erstbrutalter» mit »Brutreifealter» gleichsetzen, da ein Aufschub der Erstbrut z. B. durch Tod oder Fehlen eines (reifen) Partners in einem vorhergehenden Jahr verursacht sein kann. Bei vorsichtiger Auswertung der bisher vorliegenden Zahlen kann man aber doch sagen, dass mindestens die Hälfte der in Südbaden erstmals zur Brut schreitenden Störche dreijährig (ausnahmsweise zwei-

jährig) ist, dass also wohl wesentlich mehr als die Hälfte spätestens dreijährig brutreif ist. Die vorwiegend ostpreussischen Unterlagen bei Hornberger (1954) lassen 10.2 % dreijährige Erstbrüter errechnen, wenn man nur die klaren Fälle der Tabelle 2 (S. 145) berücksichtigt. Selbst wenn der Berechnung nur die Drei- bis Fünfjährigen zugrundegelegt werden, da eine Erstbeobachtung in höherem Alter häufig nicht einer Erstbrut gleichzusetzen sein wird, bleiben 36 Dreijährige gegenüber 85 Vier- und 95 Fünfjährigen, demnach ein Anteil dreijähriger Erstbrüter von 16.6 %. Diese Zahl ist aber eher zu hoch als zu niedrig, da es sicher auch noch ältere Erstbrüter gibt. Der Anteil dreijähriger Erstbrüter dürfte in Ostpreussen also zwischen 10 und 17 % liegen. Sauter & Schüz (1954, S. 94) haben darauf hingewiesen, dass die unterschiedliche Nachwuchsrate der Storchpaare in Südwestdeutschland einerseits und in Nord- und Ostdeutschland andererseits daran liegt, dass die Zahl der jungenlosen Paare im Südwesten wesentlich geringer ist als im Norden und Osten Deutschlands. Die nächstliegende Deutung für diesen Unterschied zwischen den beiden Populationen, nämlich der durchschnittlich frühere Eintritt der Brutreife bei den südwestdeutschen Weiss-Störchen, kann damit als bestätigt gelten.

Die vergleichsweise hohe Nachwuchsziffer der südwestdeutschen Weiss-Störche deutet darauf hin, dass die dreijährigen Erstbrüter bei der Jungenaufzucht schon ebenso erfolgreich sind wie ältere Brutstörche. Das zeigt besonders deutlich das in Südbaden aussergewöhnlich erfolgreiche Brutjahr 1957, an dem neun dreijährige Störche mit insgesamt 25 ausgeflogenen Jungen beteiligt sind: Durchschnitt also 2.77 gegenüber 2.74 bei allen südbadischen Paaren. Nicht so erfolgreich sind dagegen nach den bisherigen Unterlagen diejenigen Störche, die erst in höherem Alter erstmals zur Brut schreiten. Eine Gegenüberstellung ergibt: 15 dreijährige Erstbrüter der Jahre 1955—1958 hatten 42 ausgeflogene Junge, im Durchschnitt also 2.80. 13 vier- bis sechsjährige Erstbrüter hatten 23 ausgeflogene Junge, also durchschnittlich 1.77. Man hat danach den Eindruck, dass Störche, die aus irgendwelchen Gründen (nicht unbedingt mangelnde physiologische Reife) dreijährig noch nicht oder ohne Erfolg brüteten, auch später Schwierigkeiten haben, bei der Jungenaufzucht erfolgreich zu sein. Der einzige ältere Erstbrüter mit vier Jungen ist bezeichnenderweise der oben erwähnte Vierjährige, der dreijährig sein Gelege vermutlich in einem Unwetter verloren hat.

Während Lange (1954) für Dänemark zwei erfolgreich brütende zweijährige Störche mit zwei und vier ausgeflogenen Jungen anführt, wurden in Deutschland zweijährige Brutstörche bisher noch nicht festgestellt. Am 25. 4. 1957 traf nun W. Schnetter in Waltershofen (48.1 N 7.43 E), Kr. Freiburg (Breisgau), einen Storch an, dessen Ringnummer er am 27. 4. ablesen konnte: BB 5123. Den Ring hatte er selbst am 8. 6. 1955 im Nachbardorf Umkirch einem Jungstorch angelegt. Die Ringnummer wurde noch dreimal von Schnetter, am 7. 6. 1957 auch von G. Nauwerck und G. Zink abgelesen. Das Nest auf dem Dachfirst der Kirche ist vom Kirchturm aus etwa 40 m Entfernung gut einzusehen. Das Geschlecht des Ringstorchs konnte 1957 nicht mit Sicherheit festgestellt werden. Nach Beobachtungen 1958 (Copula)

war es das ♂ des Paares (G. NAUWERCK). Der Partner war unberingt und vermutlich ebenfalls Erstbrüter, da die künstliche Nestneuanlage erst im Frühjahr 1957 errichtet wurde, nachdem das Dorf seit 1954 ohne Storchnest war. Nach Beobachtungen des Pfarrers tauchten schon während der Anbringung des Nestes mehrere Störche auf. Vom 1.—11. 4. kämpften bis zu sieben Störche um das Nest. Ab. 12. 4. hatte sich ein Paar behauptet, das noch einmal fremde Störche abzuwehren hatte. Beginn der Brut etwa 29. 4. Weitere Beobachtungen (R = Ringstorch, U = unberingter Partner):

25. 4. (SCHNETTER): R kommt mit Zweig zum Nest, U später ohne Baumaterial, eine Copula, dann beide ab.
27. 4. (SCHNETTER): R und U im Nest, U sitzt. Kurze Abwehr eines Fremdstorchs, bei der R ausgeprägteres Abwehrverhalten zeigt als U. Später beide ab.
12. 5. (NAUWERCK): U brütet von 13.00—16.45 Uhr ohne Ablösung.
1. 6. (SCHNETTER): 17.30 Uhr U sitzt, steht in zwei Stunden sechsmal auf. Drei frischgeschlüpfte Jungvögel zu sehen. 20 Uhr Ablösung durch R, der Futter auswürgt, kurz in der Nestmulde stochert und dann die Jungen deckt.
7. 6. (NAUWERCK und ZINK): U deckt bei regnerischem Wetter von 7.45—11.45 Uhr und ebenso von 14.00—17.30 Uhr. In diesen Zeiten keine Ablösung und Fütterung durch R, möglicherweise aber zweimalige Ablösung in den Mittagsstunden. R kommt 17.30 Uhr, bringt einige Regenwürmer, U fliegt ab. Die Jungen sehen sehr kränklich und ungesund aus.
14. 6. (SCHNETTER): 4.15 Uhr R streicht bei Ankunft an der Kirche vom Nest ab, kreist eine halbe Stunde über dem Dorf, kommt aber zwischendurch zweimal kurz zum Nest. Ab 6.10 Uhr U im Nest; 6.50 Uhr erscheint R, da Fremdstorch vorbeifliegt; kurzes Drohklappern. 7.00 Uhr nach kurzem Stochern wirft R innerhalb von zwei Minuten zwei tote Jungstörche aus dem Nest. 8 Uhr U fliegt ab und bringt ein Grasbüschel, das R mehrfach vergeblich zu entreissen versucht und das dann von U eingebaut wird. Dabei zerrt U das dritte tote Junge aus der Nestmulde. R wirft es nach kurzem Zögern aus dem Nest. U fliegt ab. 8.30 Uhr R zeigt heftiges Drohklappern und Flügelpumpen einem Fremdstorch gegenüber. 9 Uhr R sitzt 13 Minuten in der Nestmulde. Nach weiteren 30 Minuten fliegt auch er ab.
16. 6. Nach Angabe des Pfarrers haben beide Störche am 16. 6. das Dorf verlassen.

Diese Beobachtungen erbringen damit erstmals für Deutschland den Nachweis, dass ein zweijähriger Storch, und zwar ein ♂, mit einem Partner unbekannten Alters ein Gelege gezeitigt und drei Junge zum Ausschlüpfen gebracht hat. Die Jungvögel sind im Alter von knapp zwei Wochen eingegangen, ganz offensichtlich weil bei dem zweijährigen Ringstorch die notwendigen Brutpflegehandlungen nicht in gleichem Masse entwickelt waren wie die physiologische Reife (SCHÜZ 1949). Besonders die Beobachtungen von 7. 6. zeigen dies deutlich: In vier Vormittagsstunden keine Fütterung durch den Ringstorch. Am Nachmittag kommt er erst nach mindestens $3\,^1/_2$ Stunden mit wenigen Regenwürmern, während fütternde Altstörche normalerweise dicke Futterballen auswürgen. Der Partner hatte keine Möglichkeit, diesen Ausfall wettzumachen, da in den ersten Lebenswochen der Jungstörche jeweils ein Altstorch am Nest Wache hält bzw. die Jungen deckt. Kommt keine Ablösung, so »kann» er das Nest nicht verlassen. Schon während der Bebrütung fiel das lange Fernbleiben des Ringstorchs auf. Da der Partner das Gelege nicht ohne Ablösung verliess,

kam es trotzdem zum Ausschlüpfen der Jungen. Erst in der Fütterrungsperiode führte das Versagen des Ringstorchs zum Hungertod der zwei Wochen alten Jungen, deren Grösse zu diesem Zeitpunkt höchstens einem Alter von acht Tagen entsprach. Das übrige Verhalten des Zweijährigen (Nestverteidigung, Nestpflege) machte einen normalen Eindruck.

Das Jahr 1958 bescherte uns zwei weitere zweijährige Erstbrüter. In Ulm (48.35 N 8.3 E), Kr. Offenburg, zog BB 5374 mit einem vierjährigen Partner drei Junge auf, von denen eines beim Flüggewerden verunglückte. Die Ringnummern dieses Paares wurden am 25. 4., 26. 4., 9. 5. und 26. 5. 1958 von G. Zink abgelesen. Der jugendliche Erstbrüter, der am 6. 6. 1956 von O. Scherwitz in Rheinbischofsheim beringt wurde, verhielt sich völlig normal. Sein Anteil an der Bebrütung der Eier und am Füttern der Jungen dürfte dem des Partners etwa entsprochen haben.

Am 3. 5. 1958 konnte Günther Müller, Karlsruhe, an einem Nest in Rastatt (Baden) (48.52 N 8.13 E) den Brutstorch BB 5391 feststellen, der von F. Morsch am 13. 6. 1956 nestjung in Ottersdorf, Kr. Rastatt, beringt worden war. Der Partner war unberingt. Auch diese Brut verlief völlig normal. Die Ringnummer BB 5391 konnte von G. Müller und E. Frey am 21. 7. 1958 kurz vor dem Ausfliegen der drei Jungen noch einmal bestätigt werden. Auch diese beiden Frühbrüter waren wahrscheinlich Männchen (Grössenvergleich mit dem Partner).

Zusammenfassung

Mehr als die Hälfte der in Südbaden erstmals zur Brut schreitenden Störche ist dreijährig. In Ostpreussen und vermutlich auch in Norddeutschland liegt der Anteil der Dreijährigen wesentlich unter 20 %. Daraus erklärt sich der Unterschied in der Zahl der jungenlosen Paare in Südwestdeutschland einerseits und im Norden und Osten Deutschlands andererseits. Die grössere Zahl jungenloser Paare in Nord- und Ostdeutschland hat zur Folge, dass die durchschnittliche Jungenzahl in diesen Gebieten beträchtlich niedriger ist als in SW-Deutschland.

Die bisher aus Baden vorliegenden Zahlen machen wahrscheinlich, dass die dreijährigen Erstbrüter bei der Jungenaufzucht erfolgreicher sind als Störche, die erst vierjährig oder später erstmals zur Brut schreiten.

In Südbaden konnte 1957 erstmals für Deutschland ein beringter zweijähriger Storch, ein ♂, als Brutvogel festgestellt werden. Es kam zum Schlüpfen von drei Jungen, die aber im Alter von etwa zwölf Tagen verhungerten. Schuld daran trug die mangelnde Reife der Brutpflegeinstinkte bei dem Zweijährigen, der nur selten und zu wenig fütterte. Der Partner konnte den Ausfall nicht ausgleichen, da er durch das stundenlange Fernbleiben des Ringstorchs an das Nest gebunden war.

1958 waren zwei zweijährige Erstbrüter, vermutlich ebenfalls ♂♂, erfolgreich. In beiden Nestern wurden drei Junge aufgezogen.

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Die südkaspische Küste als Leitlinie des Vogelzugs und als Winterquartier

Ernst Schüz

Vogelwarte Radolfzell

Wer die Landkarte nach günstigen Vogelzug-Plätzen durchmustert, wird unweigerlich an der Südküste des Kaspischen Meeres hängenbleiben. Ein 500 km langer Strand legt sich hier ungefähr quer zur üblichen Zugrichtung und fängt daher notwendigerweise den Zug auf, soweit er nicht abgelenkt ist. Diese Küstenleitlinie liegt in einer geographischen Breite, die starken Durchzug erwarten lässt, umsomehr, als das im Herbst verlassene Hinterland aus einer weitgedehnten, von grossen Scharen ziehender Brutvögel besetzten Landmasse besteht. In anderer Hinsicht ist die Lage weniger einfach: Das die kaspische Südküste begleitende, weit über 4,000 m hohe (mit 5,604 m gipfelnde) Elbursgebirge verstärkt die Riegelwirkung der nahen Uferlinie, und da sich das fernere Winterquartier infolge der Spaltung der Landmassen — hier Arabien-Afrika, dort Indien — teilt, kommen recht verschiedene Anflugwinkel des Heimzugs in Frage.

Dieser Tieflands- und Hochgebirgstrakt Südkaspiens ist wiederholt das Ziel auch ornithologisch tätiger Naturforscher gewesen: Zuerst (1770) des Samuel Gottlieb Gmelin, im 19. Jahrhundert der Eichwald, Ménétries, de Filippi, Blanford, Radde. Sarudny und Mitarbeiter (Loudon u. a.) waren im letzten Viertel des vergangenen Jahrhunderts und später dort tätig. In den letzten 50 Jahren reisten hier Woosnam, Buxton, Heinrich, Peter Scott, Paludan, Misonne, Petter, Norton. In Nord-Talysch, das wir bei unserer Betrachtung einbeziehen, machten sich auch neuerdings Fachleute aus dem russischen Raum her an die Arbeit, so Tugarinov und Koslova, Ivanov, Isakov und Worobiev und andere. Ich selbst genoss den Vorzug, von Mitte Februar bis Mitte Mai 1956 die Vogelwelt und vor allem den Vogelzug in Mittel-Gilan für die Vogelwarte Radolfzell-Rossitten studieren und, unterstützt von Präparator Manfred Wagner, für das Staatl. Museum für Naturkunde in Stuttgart sammeln zu können. Wir waren Gast bei Dr. Kudicke in Resvandeh. Eine Auswertung in Buchform *(Lit.a)* steht in Aussicht. Hier nur einige kurze Bemerkungen über den Vogelzug, während die tiergeographische Kennzeichnung der Brutvogelwelt unterbleiben soll.

Das südkaspische Tiefland ist nicht nur als Durchzugsgebiet, sondern auch als Winterquartier stark beschickt. Das Schwemmland zu Füssen des Hochgebirges ist noch vielerorts mit Buschwildnis überwachsen, die einer entsprechenden Vogelwelt Deckung gewährt. Gewaltig sind die Zahlen der dort überwinternden *Fringilla coelebs, Erithacus rubecula, Prunella modularis, T. troglodytes* und anderer Arten. Im latitudinal verlaufenden Teil der Südküste sind zwei haffartige Bildungen von besonderem Gewicht: Im Westen das 22 km lange Murd-Ab (Totes Wasser), ein bei Pahlevi in starker Strömung zum Meer ausfliessenden, flaches Südswasserhaff, und im äussersten Osten die salzige, breit gegen das Meer geöffnete Bucht von Gurgan (früher: Astarabad). Beide beherbegen in der kalten Zeit unglaubliche Massen von Anatiden aus dem Wolga- und Uralbereich und aus Sibirien. (Sie werden stark genützt, im Murdab-Gebiet durch nächtliches Käschern bei Fackelbeleuchtung und Gonggeräusch.)

Der Zug selbst, der in dem (besonders späten!) Frühjahr 1956 bei Pahlevi erst mit Beginn des März in sichtbare Bewegung kam, verdichtet sich im Strandgebiet zeitweise in grossartiger Form, während er weiter landeinwärts viel weniger auffällt. Die beste Verdichtung ergibt sich im Bereich der Nehrung, die sich vom Hafen Pahlevi etwa 18 km nach WNW erstreckt und stellenweise bis auf etwa 600 m verschmälert. Hier herrschen ganz ähnliche Bedingungen wie auf der Kurischen Nehrung. Soweit die Arten vergleichbar sind, lassen sich hier wie dort dieselben Zugregeln feststellen, und offenkundig bestehen hier wie dort entsprechende meteorologische Abhängigkeiten. Wetterbedingte Bewegungen der überwinternden oder heimkehrenden Bestände spielen eine grosse Rolle.

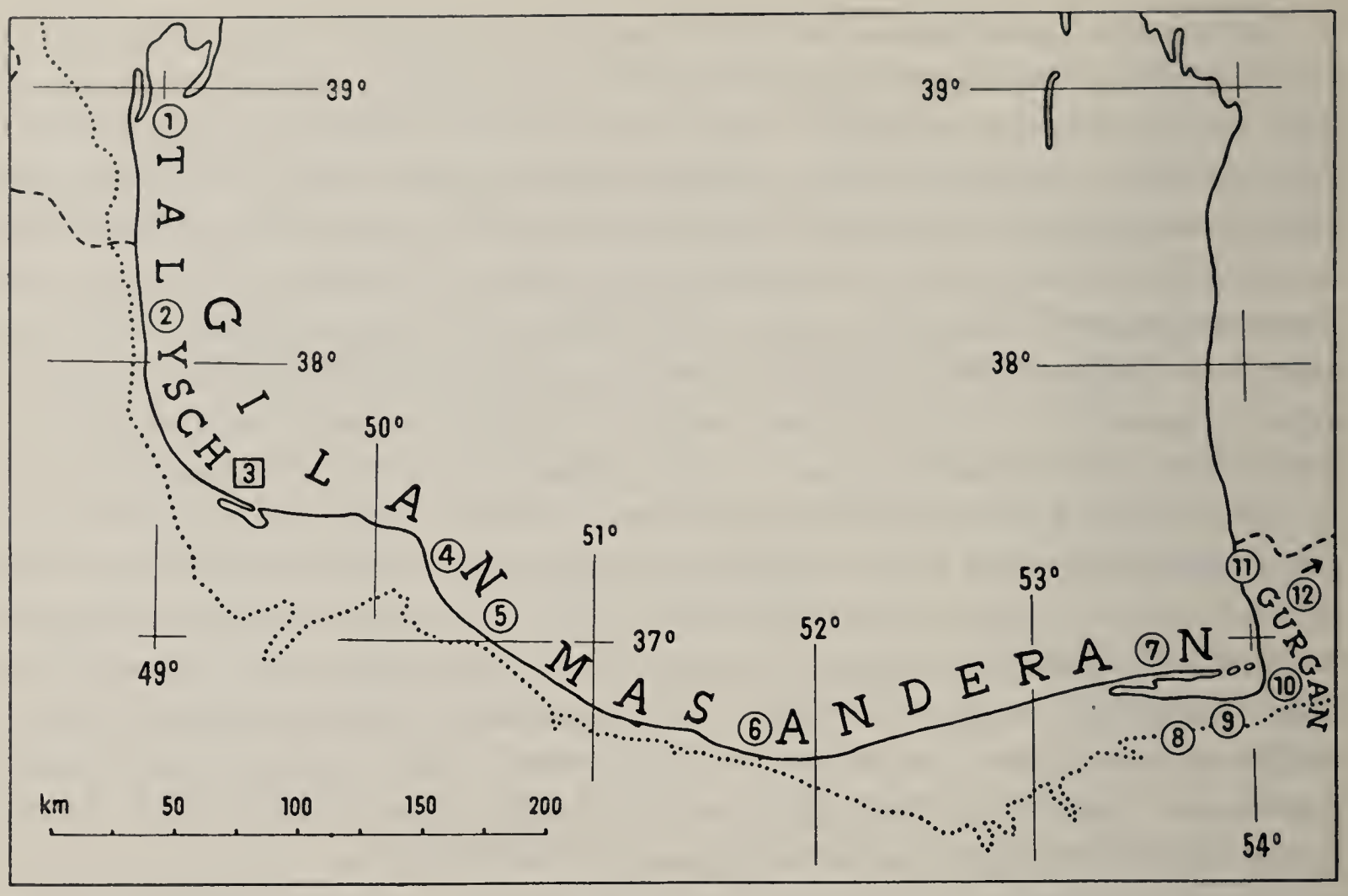
Die Übereinstimmung bei beiden Nehrungen ist insofern überraschend, als gewisse Arten am Kaspischen Meer (ähnlich oder noch mehr als an der ostpreussischen Küste) Spätwanderungen ausführen, die man so weit südlich nicht erwarten sollte. Erwähnt sei das eifrige Ziehen von *Passer montanus*, besonders aber *P. domesticus* und *P. hispaniolensis;* selbst noch am 26. April sah man Flüge des Haussperlings in Zugrichtung. *Falco tinnunculus*, hier anscheinend nicht oder nur spärlich winternd, erschien in mehreren, teils späten Schüben, der letzte offenbar am 4. Mai, wahrscheinlich nachdem *F. naumanni* schon durchpassiert war.

Die letztgenannte Art erinnert daran, dass — natürlich — das Artenbild hier 18° südlich und 30° östlich der Kurischen Nehrung nicht wenig von dieser abweicht. Das zeigt das zahlreiche Auftreten zweier *Phalacrocorax*-Arten, das Vorkommen zweier *Pelecanus*-Arten, von *Phoenicopterus, Chlidonias hybrida, Coracias*, zwei *Merops* und manchen besonderen Kleinvögeln (z. B. *Calandrella rufescens* und *C. cinerea)*. Als Winterflüchtlinge aus dem Hochgebirge im Tiefland erscheinen *Anthus spinoletta, Serinus pusillus, P. petronia* und *Emberiza cia*, und noch Anfang Mai ist *Carpodacus erythrinus* am (mindestens östlichen) Gebirgsfuss nicht selten, vermutlich nach der Ankunft aus dem SE und vor dem Aufstieg ins Hochgebirge. (Immerhin ist noch nachzuweisen, ob es sich nicht um Durchzügler aus dem Norden handeln kann.)

Rechnen wir das südkaspische Tiefland von Gurgan im Osten bis zum Westwinkel des Kaspischen Meeres und von da noch 178 km nordwärts (Talyschgebiet) bis zum Rand der Muganssteppe, so zählen wir — den untersten Gebirgsfuss bis etwa 500 m eingeschlossen — bisher 327 Arten, von denen 117 (36 %) nur Gäste sind. Diese haben ihre Heimat hauptsächlich im östlichsten Europa und im westlichsten Sibirien; über den Jenissei hinaus scheint das Herkunftsgebiet nicht zu reichen. Da die Brutvögel dieses vorgelagerten Raumes je nach mehr östlicher oder mehr westlicher Lage nicht selten verschiedenen geographischen Rassen angehören, oder da auch eine Rassenschichtung nach der Breiteverteilung vorkommt, treffen wir gerade unter den Durchzüglern eine grosse Mannigfaltigkeit an geographischen Rassen, unvergleichlich mehr als etwa auf der Kurischen Nehrung mit ihrem sehr viel beschränkteren Herkunftsgebiet. Natürlich ist das Ansprechen der Rassen oft sehr schwierig und auch umstritten und meist im Gelände ganz unmöglich. Fälle wie die der männlichen *Motacilla flava* (im Frühjahr) und *Saxicola torquata* sind Ausnahmen. An grösseren Arten bildet der Merlin einen Sonderfall; *Falco columbarius christiani-ludovici* ist ganz auffallend verschieden vom westlichen Artvertreter. Was hier an Fragen tiergeographischer Grenzlinien hineinspielt, sei hier nicht erörtert, da wir uns zu diesem Zweck hauptsächlich mit den Brutvögeln zu befassen hätten.

Was die Evolution des Vogelzugs im Gebiet anlangt, so haben hier in der (näheren) Vergangenheit offenbar keine so starken Umwälzungen stattgefunden wie etwa in West- und Mitteleuropa: Wie H. Bobek dargetan hat, waren die Klimabedingungen Südkaspiens wenigstens in der letzten Kaltzeit von den heutigen nicht sehr verschieden. Allerdings hat die Küstenlinie des Kaspischen Meeres im Lauf der Jahrtausende einen ziemlich starken Wandel durchgemacht, und es ist keine Frage, dass der Vogelzug sich diesen Änderungen plastisch angepasst hat, unbeschadet der Tatsache, dass noch heute einige Arten die hohe See in einem gewissen Umfang überfliegen, richtiger gesagt, Buchten grosszügig abschneiden *(Grus grus, Coturnix coturnix)*.

Zweifellos lohnt unser Gebiet eine weitere, gründlichere Durchuntersuchung. Wenn wir von den wiederholten Forschungen russischer Ornithologen im Küstenbereich des nördlichsten Talysch (Naturschutzgebiet Kirov, Kisil-Agatsch-Bucht) und Turkmeniens absehen, hat bisher nirgends eine längere Zeit fortlaufende planmässige Durchbeobachtung des Vogelzugs stattgefunden; auch unser Aufenthalt war darin mangelhaft, weil wir nicht täglich an der Küste weilen konnten und zu dem besten Platz, dem auf der Nehrung, zu weit hatten. Bei einem neuen Vorhaben wäre es aber wichtig, dass gleichzeitig an recht verschiedenen Punkten beobachtet werden könnte. Unter welchen Bedingungen und wo kreuzen im Frühjahr (und Herbst) die Zugvögel das Hochgebirge? Wie verhalten sich diejenigen Leitlinienvögel, die beim Heimzug auf die mittlere Zone der Südküste stossen? Woher kommen die, wie sich jetzt gezeigt hat, in Gilan gar nicht selten durchziehenden Weissstörche, und wo liegt überhaupt die Zugscheide der Indien- und der Afrikaüberwinterer beim Storch (und einigen anderen Arten)? Der südkaspische Raum ist



Südküste des Kaspischen Meeres, mit Eintragung von für die Vogelzugforschung besonders wichtigen Punkten (siehe Text). — Punktierte Linie 200-m-Isohypse; gebrochene Linie politische Grenze.

geradezu wie ein zum »Sandkastenspiel» aufgebautes Modell verschiedener Möglichkeiten des Vogelzugs, so dass hier durch eine überlegte Beobachtung gewissermassen eine Art Naturexperiment mit gutem Erfolg ausgenützt werden könnte. Auf Grund meiner Eindrücke darf ich hier an Hand einer Karte eine Anzahl Punkte herausheben, an denen eine vergleichende Beobachtung anzusetzen hätte. Das Verzeichnis beginnt mit dem Hinweis (1) auf die schon eifrig genutzten Möglichkeiten in Nordtalysch von der Kura-Mündung im Norden bis etwa Lenkoran im Süden; hier kennen sich die russischen Beobachter aufs beste aus. Iran: (2) Weiterhin verlockt das auf weniger als 3 km verschmälerte Tiefland nördlich von 38°, wo das Gebirge in steilem Hang an die Strasse tritt und in bevorzugter Weise die Erfassung aufwindliebender Grossvögel ermöglicht. Etwas südlich von 38°, südlich des Lissarflusses, könnte auch der Inselberg mit der Burgruine Lissar-Kaleh eine gute Beobachtung (freilich in einem mehr verbreiteten Tiefland) erlauben (*Lit. d*). (3) *Die Nehrung westlich Pahlevi etwa bei km 15 bis 17 würde sich als Sitz einer bleibenden Station und als eine Art Mittelpunkt für die Untersuchungen an der iranischen Küste besonders eignen*, weil hier die Verdichtung des Zuges ausserordentlich und die Übersehbarkeit des Geländes beispielhaft ist. Im Hintergrund der Nehrung und von Pahlevi selbst würde das Murdab mit seinen überwältigenden Rohrbeständen und Brutsiedlungen Aussicht für ergiebige Untersuchungen auch zur Brutzeit bieten. Die Schlammbänke an der Mündung des Siaderwischan, die man nur mit dem Boot angehen

kann, sind eine Sammelställe für rastende Laro-Limikolen wahrscheinlich zu allen Jahreszeiten. (4) Im Bereich des grossen Mündungsdeltas des Sefidrud gibt es bei Lengerud Sumpfgebiete, die zu einer näheren Untersuchung herausfordern. (5) Etwa unter 50.37 E, nicht weit westlich von dem gastlichen Ramsar, besteht zwischen Elburgsgebirgshang und Küste ein Engpass von weniger als 2 km Breite, der für Beobachtungen vorteilhaft sein muss. (6) Auch unweit des südlichsten Küstenpunktes verschmälert sich das Tiefland ein Stück weit. Hier wären Beobachtungen deshalb von Belang, weil hier die Küste die im Frühjahr vom Gebirge her kommenden Durchzügler alternativ die Richtung zu ändern nötigt, soweit sie nicht in die offene See hinausfliegen wollen. (7) Die die Bucht von Gurgan absperrende Nehrung scheint ornithologisch noch gar nicht erforscht zu sein und wäre einer genaueren Erfassung wert. (8) Die Burg von Beschar (früher: Aschraf) namens Safiabad eignet sich als hochragender Punkt vor dem Gebirgshang für Beobachtungen, mit dem Vorbehalt, dass die Breite des Tieflandes hier keine grössere Verdichtung des Zuges erwarten lässt. Dagegen stellen gewisse Plätze im Vorfeld von Beschar zu Zeiten Sammelstellen von Gänsen und anderen, weite Flächen liebenden Vögeln dar, wie P. Scott und X. Misonne beobachtet haben: Karatepe (53.26 E), Tirtasch (53.54 E) und Galugah (53.51 E). (9) Das hier nun sogleich anschliessende Bender Gas käme als Station für Küstenbeobachtungen in Betracht. (10) Wahrscheinlich noch günstiger wäre Kurd-Kui, unmittelbar dort, wo die Westost-Küste nahezu unvermittelt in eine Südnord-Küste übergeht und daher seltene Leitlinienbedingungen entstehen, worüber erste Beobachtungen von Misonne vorliegen. In der Turkmenensteppe und damit in einem — verglichen mit den bisherigen Tieflandverhältnissen — landschaftlich-ökologisch neuartigen Raum würde in Ergänzung zu Kurd-Kui ein noch näher zu bestimmender Küstenpunkt (11) nahe der Atrekmündung (also nicht weit von dem sowjetischen Schutzgebiet Hassan-Kuli), von Wert sein. Auf dem Wege dahin, noch südlich von der Küstenstadt (und Endstation der transiranischen Eisenbahn) Bender Schah hat mich bei der Durchfahrt sehr beeindruckt eine Bauminsel in der sonst baumlosen Getreidesteppe mit einer starken Verdichtung der Vogelwelt Anfang Mai *(Lit. c)*. (12) Der See Alagel (Atagel) 37.42 N 55.2 E ist nach den Beobachtungen von P. Scott ein beachtenswerter Einfallplatz von Wasservögeln.

Weiterhin sind (über Fragen des Vogelzugs hinausgehend) im Hinterlande von Gurgan die Pässe Abr (36.42 N 55.2 E) und Kosch Dschilagh (36.49 N 55.20 E) wichtig. In diesem Raum zieht eine bedeutsame vogelgeographische Scheide durch. Die weiter westlich liegenden Pässe des Elburgsgebirges sollten zur Zeit des Vogelzugs ebenfalls studiert werden.

SCHRIFTTUM

Näheres und weitere Literatur siehe (a) Schüz, Vogelwelt des Südkaspischen Tieflandes, vor dem Erscheinen (Stuttgart 1959). Bezug ist oben ferner genommen auf Schüz: (b) Vom Frühjahrs-Durchzug von *Motacilla flava* an der Südküste des Kaspischen Meers; Vogelwarte 18, 1956, S. 169—177 — (c) Vogel-Erlebnisse in einer Baum-Oase bei Bender-Schah; Beitr. Vogelk. 6, 1957, S. 75—78 — (d) »Süd-Kaspien»; Kosmos 54, 1958, S. 45—54.

Vergleichende Beobachtungen über die Balz brasilianischer Pipriden

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Der Wunsch, die Familie der Pipriden, auch Schmuckvögel oder Manakins genannt, in weiterem Rahmen einer genauen vergleichenden Beobachtung zu unterziehen, regte sich in mir, als ich 1939 in der Sumpfniederung SO-Brasiliens die eigentümlichen Balztänze von 4 von ihnen *(Manacus manacus, Pipra erythrocephala, Pipra pipra* und *Machaeropterus regulus)* zu studieren Gelegenheit hatte. Inzwischen habe ich auf beschwerlichen Reisen in die entlegensten Teile Brasiliens 19 Arten in 22 geographischen Formen lebend kennen gelernt.[1] Die wenigen, die sich bisher mit der Biologie der Pipriden beschäftigten, gingen nur auf einzelne Arten ein.[2]

Die Schmuckvögel entziehen sich durch ihren Aufenthalt in den dichtesten tropischen und subtropischen Wäldern nur zu leicht der genauen Kontrolle. Ich fand bestätigt, dass sie in vieler Hinsicht ein hervorragendes Studienobjekt für die Verhaltensforschung sind. Wir haben es hier mit einer vielseitigen Gruppe sich morphologisch mehr oder weniger nahestehender Formen zu tun, oft reich an arteigenen Verhaltensweisen, die zu vergleichen sind. Meine Ergebnisse können hier nur skizziert werden.

Die grösste Mannigfaltigkeit entwickeln die Pipriden im Amazonasgebiet, wo ich stellenweise ein halbes Dutzend verschiedener Arten in derselben Gegend antraf. Ihre Grösse schwankt zwischen der eines Goldhähnchens *(Regulus)* und der eines Neuntöters *(Lanius collurio)*, ihre typischste Ausbildung finden sie in einer Gruppe

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[1] *Piprites chloris chlorion* (Cabanis), *Pipra fasciicauda scarlatina* Hellmayer, *Pipra nattereri* Sclater, *Pipra* nova spec., *Pipra erythrocephala rubrocapilla* Temminck, *Pipra pipra cephaleucos* Thunberg und *Pipra pipra separabilis* Zimmer, *Machaeropterus regulus regulus* (Hahn) und *Machaeropterus pyrocephalus pyrocephalus* (Sclater), *Xenopipo atronitens* Cabanis, *Tyranneutes stolzmanni* (Hellmayr), *Antilophia galeata* (Lichtenstein), *Chiroxiphia pareola pareola* (Linnaeus) und *Chiroxiphia caudata* (Shaw and Nodder), *Ilicura militaris* (Shaw and Nodder), *Manacus manacus gutturosus* (Desmarest) und *Manacus manacus subpurus* Sherrie and Reichenb., *Schiffornis turdinus turdinus* (Wied) und *Schiffornis turdinus wallacii* (Sclater and Salvin), *Neopelma aurifrons* (Wied) und *Neopelma pallescens* (Lafresnaye), *Heterocercus linteatus* (Strickland). Reihenfolge der Arten nach HELLMAYR (1929).

[2] Eine Arbeit von CHAPMAN (1935) über *Manacus vitellinus* aus Zentral-Amerika scheint der erste genaue Bericht zu sein, der über die Balz eines Schmuckvogels gemacht wurde. Von der aus Mexiko bis Ekuador bekannten *Pipra mentalis* gibt SKUTCH (1949) ein vollständiges Lebensbild.

sexual-dimorpher Formen, deren Männchen mit zum schönsten gehören, was die Vogelwelt in den Tropen hervorgebracht hat. Ausserdem gibt es mehrere auch im männlichen Geschlecht schlichte Vertreter, die wir als den Anschluss der Schmuckvögel an die beiden Nachbarfamilien — die Tyrannen und die Cotingas — auffassen müssen. In einigen Fällen ist die morphologische Trennung dieser drei neotropischen Familien nicht in die Augen springend und da ist es besonders wünschenswert, unsere Kenntnisse durch Verhaltensstudien zu erweitern.

Einige Pipriden beschränken sich auf ein schlichtes, stimmliches Markieren ihres Standortes, z. B. *Tyranneutes* und *Schiffornis*. Es ist sicher kein Zufall, dass beide zu den nicht sexual-dimorphen, grünen Formen gehören, deren Zuordnung zu den Pipriden nach den üblichen Balgkennzeichen nicht eindeutig ist. Meine Eindrücke vom Verhalten der beiden Vertreter unterstreichen den — systematisch gesprochen — zwiespältigen Charakter dieser Vögel.

Bei *Neopelma*, einer weiteren grünen Form ohne allen Sexualdimorphismus, die nächstens an die Tyrannen anschliesst, finden wir die Anfänge von wirklichem Balzzeremoniell. Während sich die auf SO-Brasilien beschränkte *Neopelma aurifrons* mit blossem Stimm-Markieren begnügt, macht die zentralbrasilianische *Neopelma pallescens* von einem niedrig stehenden Ast aus spannenhohe Luftsprünge. Dabei ertönt ein dumpfer Doppelschlag, der genau wie das Hämmern eines kleinen Spechtes klingt. Das Hämmern erfolgt im Rythmus des Auf- und Niederflatterns und muss durch Anschlagen der Flügel entstehen: eine bemerkenswerte »Instrumentalmusik», erzeugt ohne besondere Spezialstruktur. In N-Mato Grosso lernte ich eine *pallescens*-Population kennen, die den Luftsprung *ohne* das Klopfen ausführte.

Auch *Neopelma* bleibt beim Tanzen immer allein. Sie wirft sich in der Luft herum und löst beim Niederlassen ein auffallendes Zweigschwanken aus. Wahrscheinlich markierte auch sie ursprünglich nur stimmlich. Erst später kamen die Luftsprünge mit Zeigen des hochgelben Scheitelsteifs, das Klopfen und das Astwackeln als optische und akustische Steigerungen hinzu. Dieses Balzverhalten ist durchaus pipridenhaft.

Wenden wir uns nun den sexual-dimorphen Gattungen zu, den eigentlichen »Schmuckvögeln», deren Männchen wohl sämtlich kollektive Tänze ausführen. Ihre Weibchen sind einfarbig grün. Da gibt es z. B. die schwarze, mit einem roten Käppchen gezierte *Pipra erythrocephala* (Abb. 1). Von einem freien Ast aus markiert sie in aufrechter Grundstellung durch helle Rufe, bis ein zweites Männchen oder auch ein Weibchen auf denselben Ast kommt. Die Männchen ducken sich, stellen sich schräg, sodass Schwanz und Bürzel halb gegen den Partner weisen und trippeln hin und her; sie zittern, springen an Ort um, stellen die Flügel vertikal hoch usw. Schliesslich macht das erste Männchen wiederholt kleine Luftsprünge — wir erinnern an *Neopelma!* — und plötzlich saust es davon, kehrt aber sofort zum Partner auf den Balzast zurück. Ist ein Weibchen anwesend und willig, so findet die Paarung statt.

Auch bei *Pipra* finden wir das Astwackeln. Im düsteren Überschwemmungswald Zentralbrasiliens lenkte es manchmal erst meine Aufmerksamkeit auf einen solchen

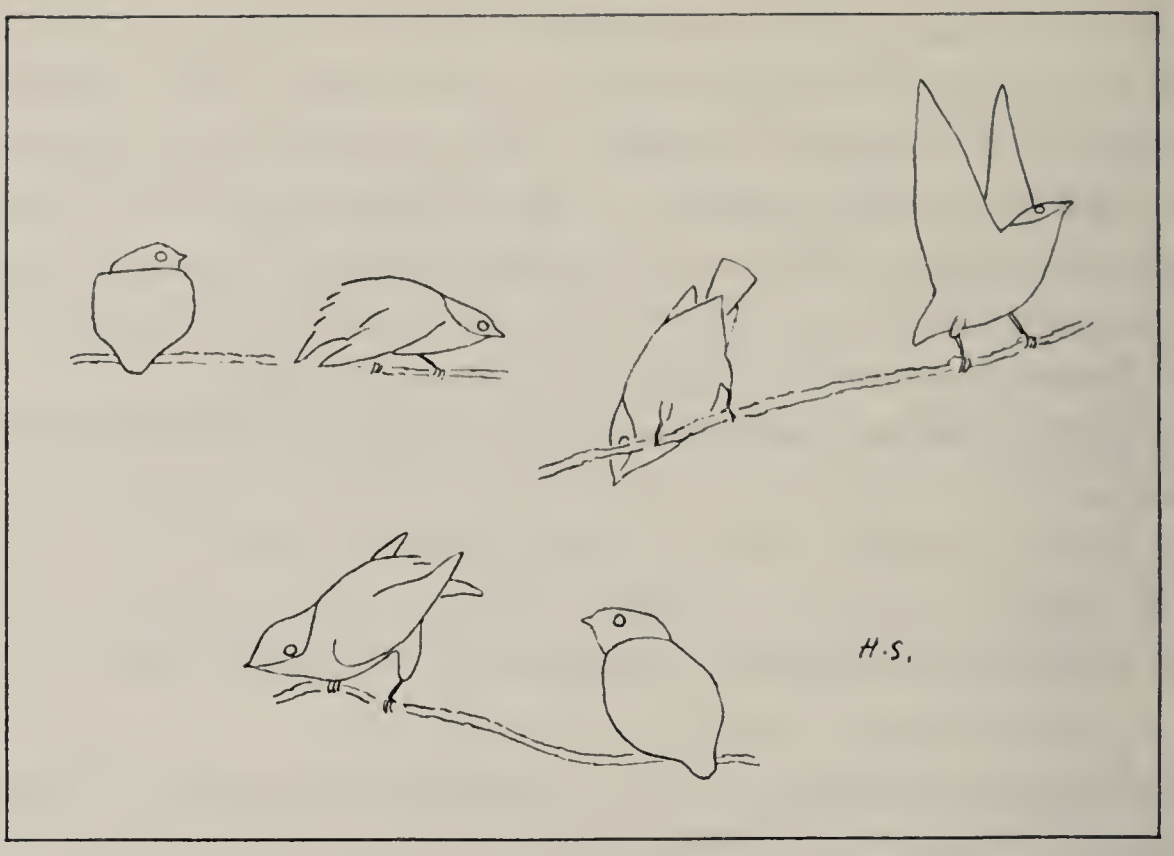

Abb. 1. Pipra erythrocephala. Tanz vor dem regungslosen Weibchen (Gruppe oben links und unten), Tanz zweier Männchen zusammen (Gruppe oben rechts). — Beachte: Fliehende Stellung der Männchen, Ducken über und unter dem Ast, Flügelheben, Hosenzeigen.

balzenden Vogel, womit ich die gute optische Wirksamkeit dieses Verhaltens testen konnte.

Bei all' diesen Zeremonien sind einige optische Signalwirkungen überzeugend. Die rote Kopfkappe wird dem Partner in der fliehenden Stellung halb von hinten gezeigt, das Vorweisen der leuchtend roten Hosen, die überraschend aus dem schwarzen Bauchgefieder auftauchen, ist besonders wirksam, wenn es nur *ein*seitig erfolgt, dem Partner zugewandt. Auch das Flügelhochheben machen die Vögel oft nur einseitig. Grüne weibchenfarbige Männchen, die noch keine Abzeichen haben, nehmen dieselben Schaustellungen ein wie die alten. Die geschlechtliche Entwicklung dieser Jungvögel ist etwa gleich derjenigen der alten, wie von mir öfter durch Abschuss nachgeprüft.

Wenn das balzlustige Männchen von *Pipra fasciicauda* mit scharfem Höhensteuer aufbaumt, ertönt erst ein kurzes Brummen und dann ein hölzern-melodischer Schlag. Das Brummen muss Flügel geräusch sein, obgleich keine Schallschwingen vorhanden sind und der Flug normalerweise nicht geräuschvoll ist. Der anschliessende Gongschlag dürfte durch Zusammenhauen der Flügel entstehen, ähnlich dem Klopfen von *Neopelma*.

Meister in der mannigfaltigsten Instrumentalmusik ist *Manacus*. Bei dem von mir studierten, schwarzweiss gefärbten *Manacus manacus* können wir nicht weniger als ein halbes Dutzend verschiedener Arten von Lauterzeugung unterscheiden, die nichts mit der Stimme des Vogels zu tun haben (»Instrumentalmusik»). Wir zählen diese Geräusche hier nach einander auf:

1. ein Rascheln, das bei jeder auch von der Balz unabhängigen Flugbewegung

automatisch auftritt. Es ist auch am toten Vogel an den Aussenfahnen der Armschwingen reproduzierbar. Bei den jungen Männchen und den Weibchen ist es nur angedeutet oder fehlt — entsprechend der geringeren Entwicklung der dazu nötigen Federstrukturen.

2. ein lautes, mit den Schallschwingen erzeugtes Schnarren, das nur in Balzstimmung hervorgebracht wird. Solche an- und abstellbare Flügelgeräusche fand ich in Brasilien auch bei anderen Vögeln mit ausgeprägten Schallschwingen der Hand, z. B. *Pipile* unter den Hokko-Hühnern.

3. vernimmt man vom balzenden *Manacus manacus* ein melodisches Brummen. Es klingt ähnlich dem Flugton mancher Kolibris und dürfte dem ebenfalls brummenden Hochschiessen von *Pipra fasciicauda* entsprechen, das ebenso an keine Spezialstruktur gebunden ist. So wird das Brummen auch von jungen *Manacus*-Männchen erzeugt.

4. und hauptsächlich verfügt *Manacus* über ein helles Knacken, das sich wie Aufeinanderschlagen zweier Kiesel anhört. Das Knacken schien mir stets mit einem Flügelhochwirbeln verbunden — sei es, dass es beim Start, bei der Landung oder im Stand vorgebracht wurde. Dieses Flügelheben erinnert an das (freilich geräuschlose) Flügelstellen von *Pipra erythrocephala*.

Gewöhnlich werden die umgestalteten Armschwingen für das Knacken verantwortlich gemacht, was auch das nächstliegende ist, da es nicht gelingt, diesen veränderten Federn eine andere, nur ihnen reservierte Funktion zuzuschreiben. Am toten Vogel ist das Geräusch nicht reproduzierbar. Gegen die Theorie des Knackens mit den verstärkten Armschwingen scheint meine Feststellung zu sprechen, dass auch die jungen grünen Männchen, welche die Umbildung dieser Federn überhaupt nicht haben, zu knacken vermögen, wenn auch etwas schwächer.

Dass das *Manacus*-Knacken kein Schnabelknappen ist, glaubt Chapman *(l. c.)* angesichts des bei Männchen und Weibchen gleichgeformten Schnabels ausschliessen zu können. Der Lautgebung nach erinnere ich mich dabei immer von neuem an ein Knochenknacken aus dem Gelenk heraus, wie es jedem Finnen vom Fussknacken der Renntiere her bekannt ist.

Schliesslich produziert der balzlustig aufbaumende *Manacus*, auch die grünen Männchen, (5.) das schon bei anderen Pipriden beschriebene dumpfmelodische Flügelzusammenhauen und das (6.) von weitem hörbare Fuss-Aufschlagen, dieses gelegentlich verbunden mit Astschütteln.

Die Erscheinung des balzenden *Manacus* ist derjenigen einer *Pipra* ganz entgegengesetzt (Abb. 2.) Die Hauptsache ist bei *Manacus* das prahlerische Zeigen des mächtigen, nach vorn gesträubten schneeweissen Kinnbartes. Im Gegensatz zu *Pipra* fusst der balzende *Manacus* meist an vertikalen Hölzern.

Die balzgestimmten *Manacus manacus* versammeln sich zu mehreren in bevorzugten Gebüschen, wo sie unter fortwährendem Rufen, Knacken, Knattern, Schnarren, Brummen, Flügelklappen und Fussaufschlagen wild durcheinander fliegen und springen. Aus diesem Trupp sondert sich alsbald ein Männchen ab und bezieht einen

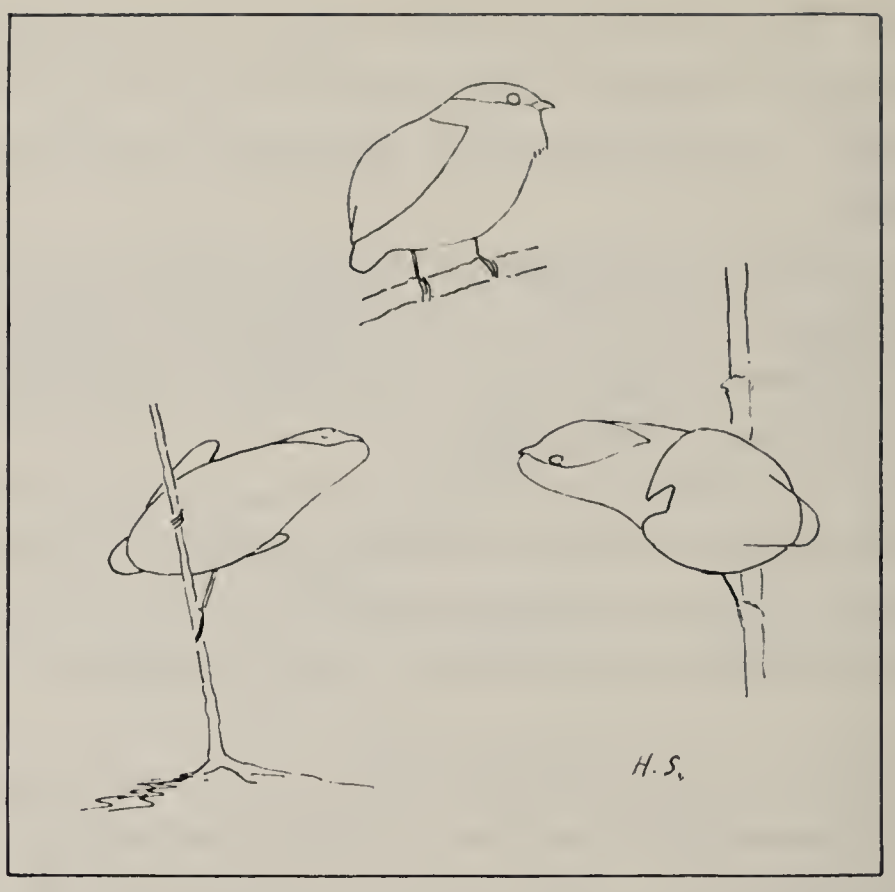

Abb. 2. Manacus manacus. Oben: Grundstellung des Männchens, nicht balzbetont. Unten: Männchen am Solotanzplatz in Bodennähe, Ansicht von unten (links) und von oben (rechts). Beachte: vertikale Aufhängung, Bart vor den Schnabel gesträubt, Zurücktreten des Oberkopfes, weisser Schulterfleck.

der in der Nähe liegenden, dicht über dem Boden befindlichen Solo-Tanzplätze. In einem rohen Dreieck springt es hier zwischen 2 bis 4 festen Stationen umher. Die strenge Gleichmässigkeit der Bewegungen des Solo-Tänzers wird durch das scharfe Metronom-Knacken, das bei jedem Sprung buchstäblich den Takt schlägt, stärkstens unterstrichen. Das Knacken kommt umso klarer und aufreizender heraus. als bei dieser rhythmischen Sprungbalz das Flügelrascheln wegfällt. Dieser Solo-Tanz erscheint wie eine Kristallisierung aus der verworrenen Gemeinschaftsbalz vieler Individuen der Art. So haben wir hier den eigenartigen Fall, dass die Entwicklung, die sicher ursprünglich von einer solitären zu einer kollektiven Balz geführt hat, sekundär wieder auf ein solitäres Zeremoniell zurückkommt. Interessanterweise wird bei dem Solo-Tanz auf jegliche Stimmäusserung verzichtet — völlig zu gunsten der eindrucksvolleren Intonierung mit Instrumentalmusik.

Den höchsten Grad wohlorganisierter Gemeinschaftsbalz legt *Chiroxiphia* an den Tag. Als Beispiel diene hier die von N-Argentinien bis SO-Brasilien verbreitete *Chiroxiphia caudata* (Abb. 3.)

Ein Männchen markiert mit lautem Ruf, bis zwei ja drei Artgenossen herbeischiessen, nicht nur alte Männchen, die im schönsten Hellblau, Rot und Schwarz prangen, sondern auch ein grünes Stück mit rotem Käppi. Unter tiefen Rufen setzen sich alle ganz dicht neben einander auf einen schrägen Ast, der grüne Vogel zu oberst. Die drei alten Männchen trippeln schnellstens an Ort, unter Zittern des ganzen Körpers. Sie wirken dabei wie *eine* vibrierende Masse, ihre Rufe erinnern an fernes Krötenkonzert. Das grüne, oben sitzende Männchen ist dagegen in aufrechter Stel-

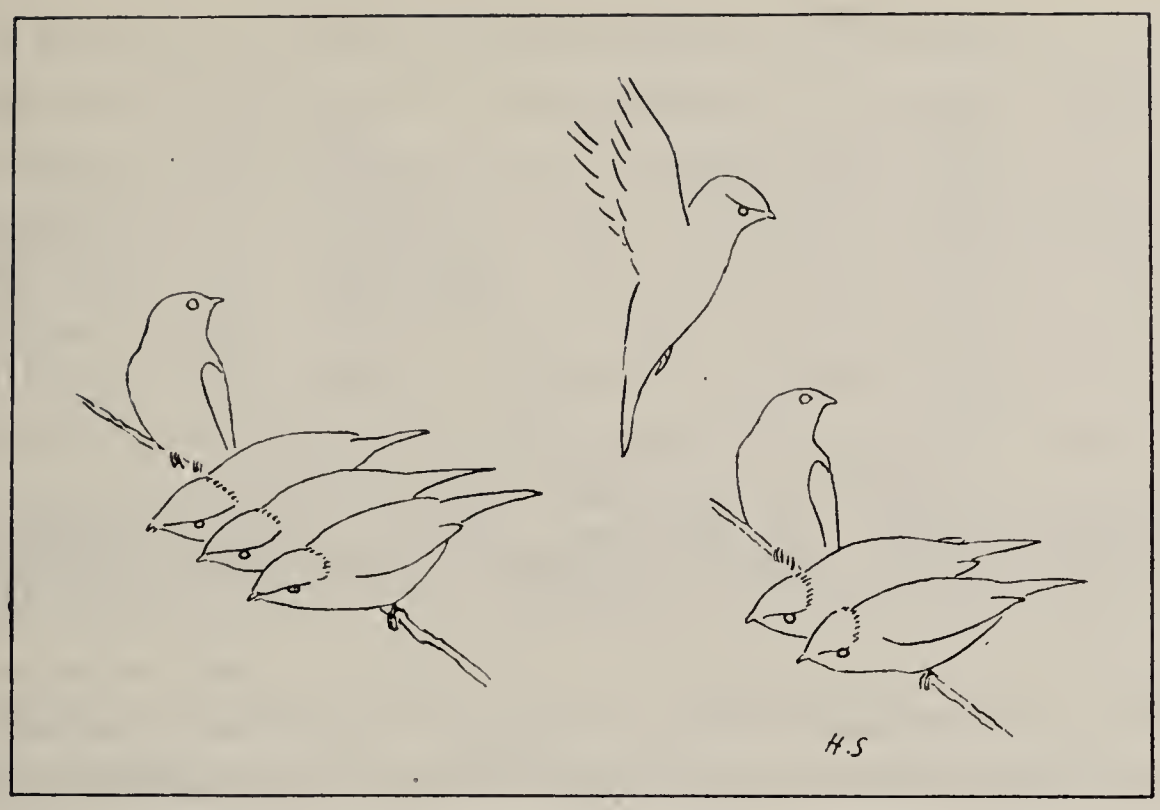

Abb. 3. Chiroxiphia caudata. Zwei Phasen des Tanzes von 3 alten Männchen vor einem regungslos dabeisitzenden Weibchen (dieses kann auch durch ein junges Männchen ersetzt werden). Links: Alle 3 Männchen trippeln geduckt an Ort und summen. Rechts: Das oberste Männchen hat sich zum Rüttelflug erhoben, die unteren Männchen trippeln und summen weiter.

lung erstarrt. Plötzlich erhebt sich das unterste Männchen zu einem spannenhohen Flug über der Gruppe. Es wendet sich den Tanzgenossen zu und rüttelt einen Augenblick über ihnen, währenddem es ein durchdringendes Pfeifen ausstösst. Darauf lässt es sich unterhalb von dem regungslosen grünen Vogel nieder. Alsdann startet das jetzt zu unterst trippelnde Männchen zum Rüttelflug — und so geht das Spiel unter dauernder Ablösung weiter, in maschinenmässig gleichförmigem Abrollen.

Diese Zeremonie kann nicht anders als eine Vorführung vor dem erstarrt zuschauenden Vogel aufgefasst werden, der, streng genommen, ein Weibchen sein müsste. Ist kein Weibchen zur Stelle, so wird Ersatz geschaffen durch ein Männchen und zwar vorzugsweise ein weibchenfarbiges junges Stück (Sick 1942). Es wird aber auch ohne Zuschauer, z. B. unter drei alten Männchen, getanzt. Das Trippeln und Seitrutschen erinnert an *Pipra*, ebenso das Umspringen.

Was wir an *Chiroxiphia* besonders zu bewundern haben, ist die Entwicklung einer kollektiven Balz mit streng verteilten Rollen und der mimischen Nachahmung des passiven Weibchens durch gewisse, dazu gleichsam abkommandierte Männchen. Die Verhältnisse bei *Chiroxiphia* lassen den Vergleich mit dem Balzverhalten bestimmter Paradiesvögel als besonders interessant erscheinen.

Wir kommen jetzt zu der letzten Form, die ich hier behandeln will: *Machaeropterus* (Abb. 4.). Das balzende Männchen hängt sich seitlich an dünne, senkrecht gestellte Zweige, den Kopf nach unten und lässt dabei ein feines Schwirren hören. Diese Strophe ist mit dem Gesang eines Schwirls *(Locustella)* vergleichbar. Ich hatte an Ort und Stelle kaum Zweifel, dass es sich dabei um Stimmlaute und nicht um

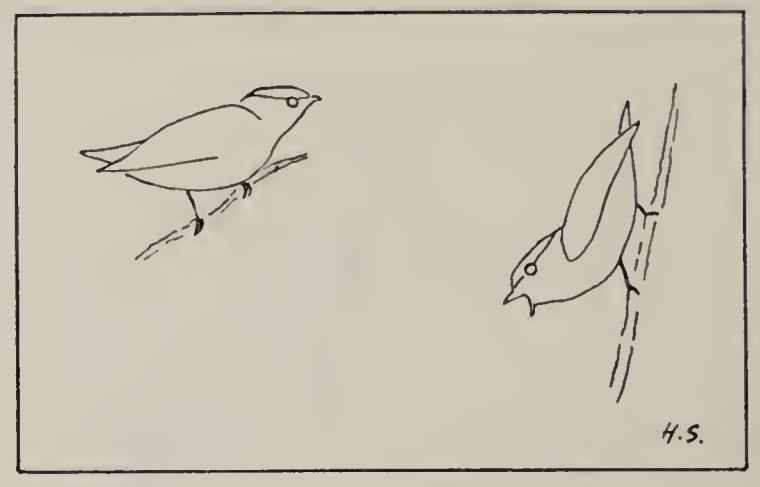

Abb. 4. Machaeropterus regulus. Ein Männchen, kopfunter aufgehängt, schwirrt mit leicht abgehobenen Flügeln und weit geöffnetem Schnabel. Ein zweites Männchen schaut still von oben zu.

eine andere Art von Geräuscherzeugung, etwa ein Flügelwetzen, handelte. Ich sah, dass der Vogel während dem Schwirren den Schnabel weit geöffnet hatte.

Machaeropterus pyrocephalus (nicht *Machaeropterus regulus*) hat einen laut klingelnden Flug. Die verantwortliche Struktur für die Erzeugung von Instrumentalmusik haben wir bei ihm in den höchst merkwürdig verbogenen und verstärkten inneren Armschwingen zu suchen, deren Kiele wie kleine Resonanzkörper aufgebläht sind. Das *pyrocephalus*-Männchen demonstriert die Fähigkeit seiner Armschwingen zu tönen sogar beim Putzen: wenn es sich schüttelt, entsteht ein helles Klappern — offenbar durch Aneinanderschlagen der Federn innerhalb ein und desselben Flügels. Der Armschwingenbereich ist bei *pyrocephalus* auch optisch besonders hervorgehoben: ein grosses weissgraues Feld, dessen Rand mit schwarzen Augenflecken besetzt ist. Dieses Signal ist am besten bei zusammengefaltetem Flügel in Rückenansicht wirksam. Tatsächlich bemerkte ich bisher während der Balzi dieser Art kein Flügelöffnen. *Machaeropterus* vollführt ein blitzschnelles Umspringen, das manchmal wie eine Riesenwelle um den Ast aussieht. Elemente wie Ducken, Zittern, Umspringen verbinden ihn mit anderen Pipriden. Zur Balz treffen sich zwei oder mehr *Machaeropterus*-Männchen.

Zum Abschluss sei eine kurze theoretische Betrachtung angestellt, anknüpfend an das immer wieder erwähnte *grüne Weibchen- und Jugendkleid* der Pipriden. Es wird oft davon gesprochen, dass die Ähnlichkeit der Weibchen vieler Schmuckvögel so gross sei, dass man besondere Mechanismen annehmen müsste, die verhindern, dass versehentlich artfremde Weibchen als natürliche Partner angesehen werden. Diese Sorge um die Reinerhaltung der Art dürfte nur einige Theoretiker bedrücken, denn: *erstens* suchen bei den Pipriden, zu mindesten bei den sexual-dimorphen, nicht die Männchen die Weibchen auf, sondern umgekehrt die Weibchen die Männchen. *Zweitens* gibt es in demselben Biotop nicht alle diejenigen Formen, die man auf dem Tisch neben einander legen kann, die Arten treffen sich also gar nicht, und *drittens* sind die Weibchen im Leben — selbst für unsere stumpfen, nicht vom Instinkt geleiteten Sinne — in Gestalt und Verhalten meist sehr wohl zu unterscheiden. Die so oft postulierten interspezifischen Verwechslungen kommen meines Erachtens nach

gar nicht in Betracht, wie auch das Fehlen sicherer Bastarde beweist. Die Tatsache, dass Schmuckvogel-Männchen mit ausgestopften, am Balzplatz angebotenen Weibchen einer anderen Pipridenart kopulieren, beweist nicht viel mehr als die Bedeutung der Bewegungslosigkeit des richtig placierten Partners für die Begattung der Pipriden.

Die Bestätigung der Tatsache, dass sich zu mindesten bei den sexual-dimorphen Pipriden Männchen und Weibchen nur auf dem Tanzboden treffen, und dass diese Lokale nie von anderen Schmuckvogelarten aufgesucht werden, ist der Schlüssel zum Verständnis vieler uns hier beschäftigender Fragen. Die Weibchen sind darauf abgestimmt, dass sich die Männchen vollständig der Balztenne widmen und also gar keinen Anteil an der Familie nehmen. Neben ihrer Sorge für Nest und Junge treffen die Weibchen die Männchen nach Belieben an den Balzästen und es ist anzunehmen, dass es bei dieser Entwicklung zur Polygamie zu mehr Kopulationen kommt und wohl auch zur Erzeugung einer grösseren Nachkommenschaft als bei Ehigkeit.

Huxley (1938) hat unter dem Gesichtspunkt der geschlechtlichen Zuchtwahl dargetan, dass solche Verhältnisse zur Vervollkommung von Farbenpracht und vielseitigem Zeremoniell der Männchen wesentlich beitragen können. Der auf die Weibchen ausgeübte Selektionsdruck ist gerade entgegengesetzt: sie beharren in ihrem ursprünglichen kryptischen Kleid, das sie im tropischen Wald mehr als sonstwo wie eine Tarnkappe schützt — das Kleid, welches wohl am besten den Familientypus widerspiegelt.

Summary

A survey is given on the courtship of 10 different species (7 genera) of manakins [1], which the author has been studying in Brazil; altogether 19 species (12 genera) have been examined (complete list see note 1 on page 672). There is noted an evolution from simple solitary courtship *(Tyranneutes, Schiffornis, Neopelma)* to the more complicated collective courtship displays *(Pipra, Manacus, Chiroxiphia, Machaeropterus)*. The highest development is shown by *Manacus* and *Chiroxiphia: Manacus manacus* by its ability to produce 6 different kinds of noises without making use of its voice, and *Chiroxiphia caudata* by a most complicated collective courtship with casted parts and mimic imitation of the passive female by certain males »ordered off» for it. Paralleling the perfection of the collective courtship are the embellishment of the males and a raising of extravagance in their behaviour at the courtship dances, whereas the females stick to a plain cryptical garment. As sexual intercourse (polygamy) is practiced only at the courtship assemblies — which are never frequented by more than one species of manakins and where the female chooses the male — the similarity of the females of different species of manakins does not seem to offer any special identification problem.

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[1] *Tyranneutes stolzmanni, Schiffornis turdinus, Neopelma aurifrons, Neopelma pallescens, Pipra erythrocephala, Pipra fasciicauda, Manacus manacus, Chiroxiphia caudata, Machaeropterus regulus* and *Machaeropterus pyrocephalus.*

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Vorderhirn und Anpassungstypus

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Wenn ein Organ auf seine Rolle im Anpassungsvorgang geprüft werden soll, so ist die Kenntnis seiner Funktion im Leben des Tieres Voraussetzung.

Je vielschichtiger und komplexer die Aufgaben eines solchen Organs sind, desto schwieriger werden Antworten auf die Frage nach seiner Bedeutung für die Erhaltung und Evolution der Lebensform. In ganz besonderem Masse gilt diese Schwierigkeit für das komplizierteste Organ, welches die Natur hervorgebracht hat, nämlich für das höchste Nervenzentrum, das Vorderhirn der höheren Wirbeltiere.

So wichtig das Grosshirn für sämtliche Leistungen des Tieres als Koordinationsmechanismus auch sein mag und so gut wir seine Leistungen im Lebensablauf auch erahnen, so wenig wissen wir bis heute über seine subtileren Funktionen. Welche seiner Teile bestimmte Tätigkeiten im Vogelkörper steuern, ist eine Frage, die von den experimentierenden Zoologen zwar gestellt wurde, die aber noch keine befriedigende Antwort gefunden hat.

Die bisherigen, auf Grund von Exstirpationsversuchen erkannten Tatsachen lassen seine Aufgaben kurz wie folgt umschreiben: Das Vorderhirn der Vögel ist ein Integrationsorgan welches verantwortlich ist für den richtigen Ablauf der für den Vogel so charakteristischen Instinkthandlungen wie Balz, Begattung und andere soziale Instinkte, dann aber auch für die freieren Aktivitäten im Vogelleben, für jene plastische Komponente des Verhaltens, welche im Lernakt und einsichtigen Handeln ihren Ausdruck findet.

Das Vorderhirn steuert und koordiniert somit wesentlich das Verhalten und wie Tinbergen sagt: »it is the coordination of mechanism and objective purpose that brings about adaptiveness of behavior».

Das Vorderhirn wirkt bei diesem Geschehen insofern mit, als es die fixierten oder stereotypen Handlungen im richtigen Zeitpunkt spielen lässt, resp. das Tier in Situationen bringt, welche solche Handlungen auslösen, und indem es als Sitz des Gedächtnisses die Erfahrungen speichert welche das plastische und anpassungsfähige Verhalten der Vögel neben den starken Instinktbindungen ermöglichen.

Wenn auch, wie schon erwähnt, die Arbeitsweise des Vorderhirns im Einzelnen so gut wie unbekannt ist, so darf doch auf Grund seiner allgemeinen Bedeutung im

Leben des Tieres die Hypothese aufgestellt werden, dass morphologische Eigenschaften im Vorderhirn vorhanden sein müssen, welche gewissermassen das strukturelle Aequivalent der Verhaltensstufen- und typen darstellen.

Die quantitativen Untersuchungen von PORTMANN zeigen, wenn auch erst in allgemeinen Zügen, dass solche Zuordnungen in der Tat nachweisbar sind.

Die hochevoluierten Papageien und Singvögel weisen eine relativ weit grössere Hemisphärenmasse auf, als die niedrig evoluierten Hühnervögel.

Ich bin überzeugt, dass gerade die plastische Komponente im Verhalten der höher evoluierten Vögel, wie Singvögel und Papageien, an sich adaptativ ist, und dass das Vorderhirn darum in ganz besonderem Masse für die progressive Evolution verantwortlich ist. So glaube ich, dass unter den Nesthockern gerade die Passerinen zur weiten Verbreitung und intensiven Artbildung schreiten konnten, weil bei dieser Gruppe einerseits keine auffälligen Spezialisierungen auftraten, und andererseits im Zusammenhang mit der veränderten Brutbiologie, auch das Integrationsorgan Vorderhirn eine Vervollkommnung erfuhr.

Wenn bereits die quantitative Untersuchung Korrelationen zwischen Hirnmasse und Verhaltensstufe oder -weise aufzudecken vermag, dann ist anzunehmen, dass die qualitative Analyse noch tiefere Einsichten in die Beziehung Vorderhirn-Verhalten und auch in der Anpassungsfrage ermöglicht.

Es scheint mir deshalb meine Hauptaufgabe zu sein, in den folgenden Ausführungen die neuesten Ergebnisse der Differenzierungsanalyse vorzulegen, welche, wie ich hoffe, einerseits die Grundlage für die experimentelle Prüfung, andererseits die Grundlage für die Frage nach dem Adaptationswert von morphologischen Vorderhirnmerkmalen bilden können.

Ein erster Weg zum Verständnis der klassentypischen Differenzierung des Vorderhirns führt über den Bauplanvergleich Reptilien-Vögel. Fig. 1 zeigt links oben das Vorderhirn eines Reptils *(Lacerta)*, links unten das Vorderhirn eines niedrig evoluierten Vogels (Taube). Die Hemisphären sind in dieser Darstellung sagittal geschnitten und zeigen die wichtigsten differenzierungsmässig verschiedenen Zellgebiete.

Das Bild will zeigen, welche Teile der Vogelhemisphäre schon bei den Reptilien in voller Ausbildung vorhanden waren, welche anlagemässig da waren und welche Gebiete neu strukturiert oder gar neu gebildet wurden.

Wir unterscheiden beim Reptil zwei basale Gebiete, das Palaeostriatum und das Archistriatum und das phylogenetisch jüngere, dorsal kappenförmig über den basalen Gebieten liegende Neostriatum. Eine kleine Zone im Pallium der Reptilienhemisphäre, welche vorne, median in der Nähe des Abganges des Tractus olfactorius, in der rostralen Fortsetzung des parahippocampalen Cortex liegt, das sogenannte Primordium Neopallii, gilt als Anlage des im Evolutionsschritt Reptil-Säugetier mächtig werdenden Neocortex.

Bei den Vögeln führt die stammesgeschichtliche Entwicklung über die im beigefügten Schema dargestellte hypothetische Stufe (Grundtypus) zum Differenzierungs-

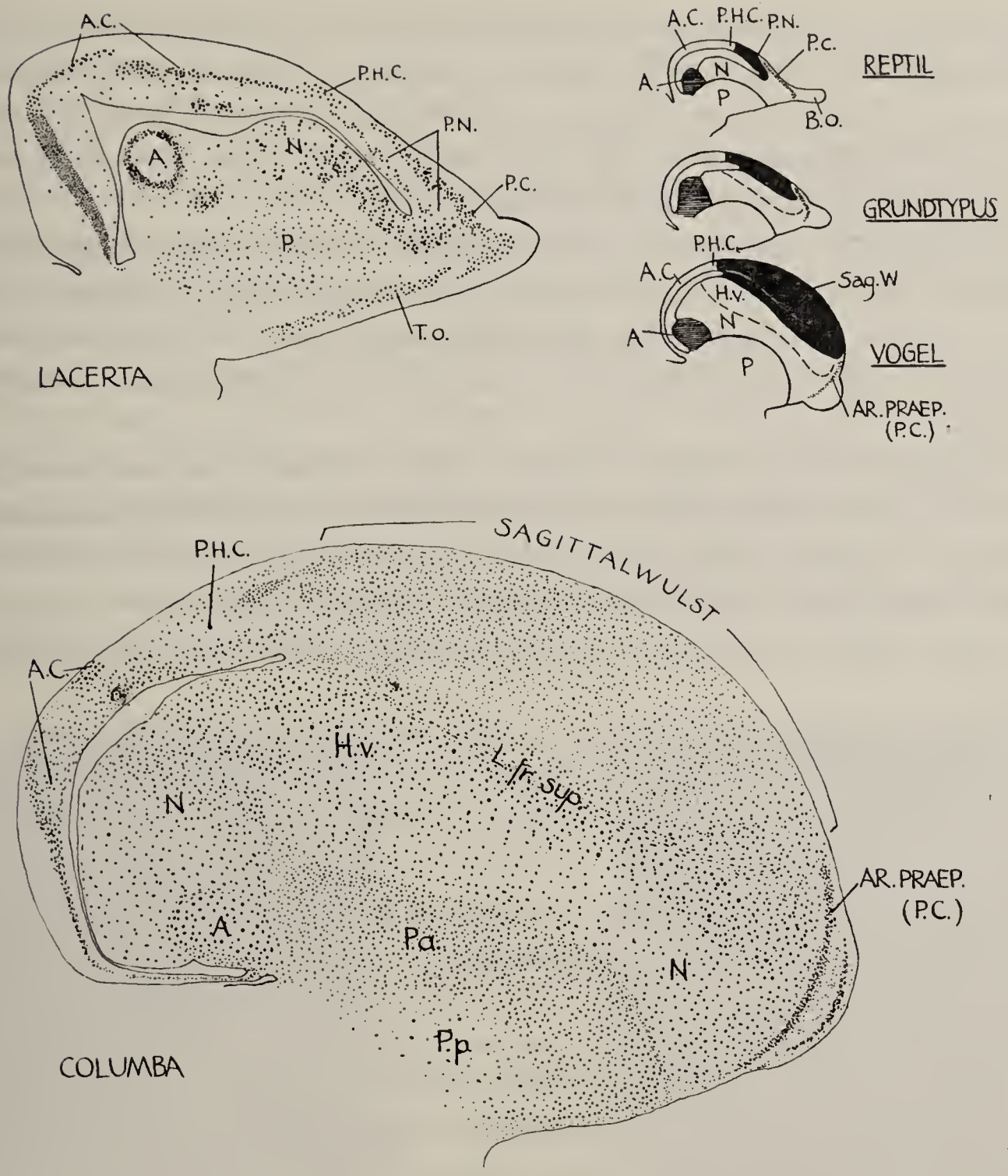

Fig. 1. Die Differenzierungs- und Massenzunahme im Evolutionsschritt Reptil-Vogel. *Links oben:* Parasagittalschnitt durch die Hemisphäre von *Lacerta muralis. Links unten:* entsprechender Schnitt durch die Taubenhemisphäre. *Rechts oben:* schematische Darstellung der Hemisphärenevolution. Der Grundtypus stellt einen hypothetischen Differenzierungszustand dar, welcher zwischen Reptilien- und Vogelstadium vermittelt.

Abk.: A. Archistriatum, A.C. Archi-Cortex, Ar. Praep. Area praepyriformis, B.o. Bulbus olfactorius, H. V. Hyperstriatum ventrale, L. fr. sup. Lamina frontalis superior, N. Neostriatum, P. Palaeostriatum, Pa. Palaeostriatum augmentatum, P. H. C. Parahippocampaler Cortex, P. C. Palaeo-Cortex, P. N. Primordium Neopallii, P. p. Palaeostriatum primitivum, Sag. W. Sagittalwulst, T. o. Tuberculum olfactorium.

typus der Taubenhemisphäre. Beim Vogel finden sich wieder in entsprechender Lage die beiden basalen Gebiete Archi- und Palaeostriatum.

Das phylogenetisch neuere Gebiet hingegen, das Neostriatum, hat sich in zwei zellulär verschiedene Zonen differenziert, in das eigentliche Neostriatum und in das kappenförmig darüberliegende Hyperstiatum ventrale.

Eine besonders starke topographische und differenzierungsmässige Umbildung hat sich im Bereich des Mantels vollzogen.

Hippocampus und Parahippocampusgebiet sind in die caudale Hälfte der Hemisphäre gedrängt und cortical differenziert, während aus dem in der rostralen Fortsetzung des Parahippocampus liegenden Primordium Neopallii (eventuell auch aus Anteilen des Parahippocampus) sich ein mächtiges, massiges, also nicht corticales Gebiet, der sogenannte Sagittalwulst, entwickelt hat.

Dieses Kerngebiet, welches wie ontogenetische Untersuchungen bewiesen haben, neopallialen Ursprungs ist, ist mit dem unter ihm liegenden Hyperstriatum ventrale dh. also mit dem erweiterten Basalganglion verwachsen und hebt sich bei allen Vögeln als mehr oder weniger deutlicher Längswulst von der dorsalen Hemisphärenoberfläche ab.

Der Ventrikel wird durch diese Verwachsung von Neopallium und Basalganglion zu einem schmalen medianen Spalt und zu einem wenig ausgedehnten caudalen Seitenhorn reduziert. Ebenfalls stark reduziert ist der palaeopalliale Cortex, welcher sich auf eine kleine Zone hinter dem Bulbus olfactorius (Area praepyriformis) und auf eine caudale Zone, welche lateral über dem Archistriatum liegt, (Periamygdalare Zone) beschränkt.

Wie in der Zeichnung sichtbar wird, neigt der Sagittalwulst schon bei den primitiveren Formen zur zellulären Untergliederung; bei den hochcerebralisierten Vögeln gliedert er sich deutlich in mehrere differente Kernzonen: Die Schichtstruktur wird intensiviert.

Wir stellen also fest, dass in der Hemisphäre Differenzierungen und Neubildungen beim Übergang Reptil-Vogel stattfinden, die insbesondere die oberen und vorderen Teile des Vorderhirns ergreifen. Wir dürfen also mit Recht behaupten, dass, wenn im Vorderhirn überhaupt Merkmale gefunden werden sollen, welche die Evolution des Vogels begünstigten, also selektiv wirksame Merkmale, sie in diesen Bezirken gesucht werden müssen. Neostriatum, Hyperstriatum und Wulst bilden die Hauptmasse der Hemisphäre; in ihnen sind mit grösster Wahrscheinlichkeit die Integrationsmechanismen zu lokalisieren, welche die mehr als nur reptilienhaften Möglichkeiten des Vogeldaseins ausmachen.

Die histologische Analyse hat den Nachweis erbracht, dass in den dorsalen Gebieten, Wulst, Hyperstriatum ventrale und Neostriatum Evolutionsprozesse in der Vogelklasse stattgefunden haben, welche erlauben solche Korrelationen zwischen Hirnstruktur und Verhaltensstufe zu suchen.

Archistriatum und Palaeostriatum sind bei allen 51 von mir untersuchten Vogelarten von nahezu identischer Struktur und ihre Ausdehnung in der Evolutionsreihe relativ zu den Dorsalgebieten abnehmend. Die dorsalen Gebiete sind im Gegensatz zu den basalen Gebieten zellulär sehr variabel differenziert; sie zeigen enorme Unterschiede in ihrer Proportion und in ihren Lageverhältnissen zu den basalen Gebieten.

Zur Differenzierung: Wenn beim Übergang von einem der kappenförmig übereinander liegenden dorsalen Gebiete bei einer Taube, Seeschwalbe oder auch bei andern indexniedrigen Formen nahezu keine Differenzierungsunterschiede aufzuweisen

sind, der dorsale Gebietskomplex im ganzen eher homogen erscheint, dann sind bei indexhohen, hochevoluierten Formen wie Singvögeln, Papageien, Eulen diese zellulären Differenzierungssprünge stark ausgeprägt.

Fig. 2 zeigt diese Unterschiede der Schichtstruktur am Bsp. der Taube und einer Eule. Man erkennt, dass sich die dorsalen Gebiete bei der Taube in der zellulären Differenzierung nur wenig unterscheiden, dass hingegen bei der Eule die Schichtstruktur sehr deutlich wird, indem die Zellgruppierungen, die Zellgrösse und Zelldichte von Gebiet zu Gebiet stärker variiert.

Ausser der erwähnten Intensivierung der Schichtstruktur durch Ausprägung der Gebietscharaktere zeigt diese Darstellung auch, dass der ursprüngliche, z. B. bei der Taube nahezu homogene Wulst, beim Steinkauz drei distinkte Gebiete aufweist, dass also nicht nur die Gliederung intensiviert, sondern auch die Zahl der Schichten erhöht wird.

Eine solch intensivierte Schichtstruktur weisen auch die Passerinen, die Psittaci überhaupt sämtliche indexhohen Formen auf.

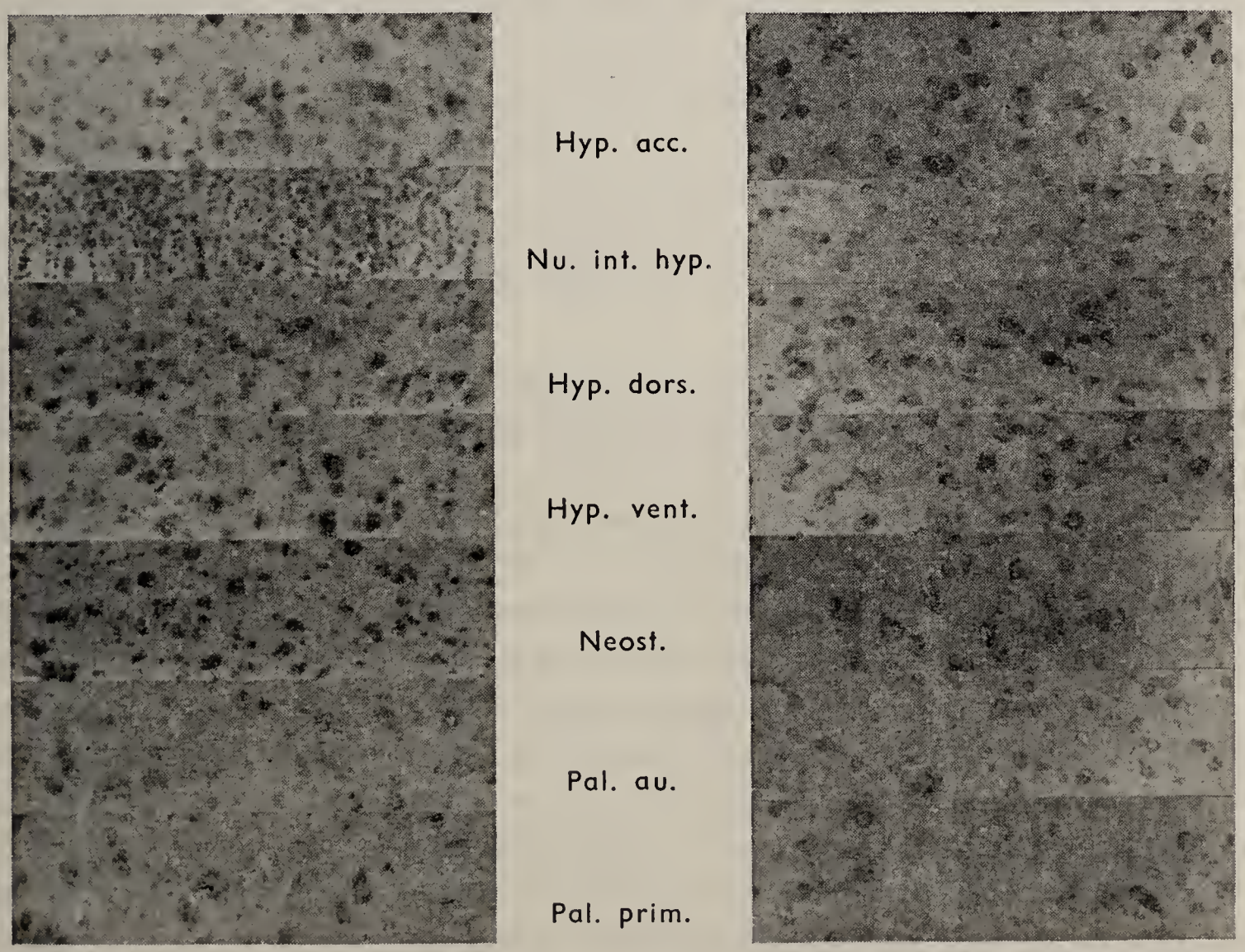

Fig. 2. Intensivierung der Schichtstruktur von niedrig zu hochevoluiertem Vogel. *Taube:* Hemisphärenindex ca. 3.;, *Steinkauz:* Hemisphärenindex 12.9.

Abk.: Hyp. acc. Hyperstriatum accessorium, Hyp. dors. Hyperstriatum dorsale, Hyp. vent. Hyperstriatum ventrale, Neost. Neostriatum, Nu. int. hyp. Nucleus intercalatus hyperstriati, Pal. au. Palaeostriatum augmentatum, Pal. prim. Palaeostriatum primitivum.

Die Lage dieser dorsalen Gebiete ist sehr variabel ebenso wie ihre Proportion innerhalb der Hemisphäre. Zunahme der relativen Masse einzelner Bezirke des dorsalen Gebietskomplexes bedeutet, dass die Hemisphäre oberflächlich gestaltet, skulpturiert wird.

Es sind insbesondere die indexhohen Typen, welche extreme Skulpturierung aufweisen.

Der Vergleich der Formen zeigt, dass zwei Zonen für die gestaltliche Typifizierung der Hemisphären massgebend sind:

1. Das phylogenetisch jüngste Gebiet, das Sagittalwulstgebiet, welches, wie der Name sagt als Wulst je nach Masse mehr oder weniger von der dorsalen Hemisphärenfläche sich abhebt.

2. Die frontale Zone von Neo- und Hyperstriatum ventrale, welche ebenfalls sehr starke Massenunterschiede aufweist und die Hemisphärengestalt mitbestimmen kann.

Ausgehend von einer gestaltlich primären Vorderhirnform stellen wir fest, dass nur zwei qualitativ verschiedene Skulptursukzessionen in der Vogelklasse in Wirklichkeit vorkommen: Da ist einmal eine erste Reihe, in welcher die frontalste Zone des Neo-Hyperstriatum sukzessive nach unten gedrängt wird durch den sich in die Breite und nach vorne ausdehnenden Wulst. Diese Verlagerung der Wulstmasse in die Front bezeichnen wir als *dorsale Frontbildung*. Ferner findet sich eine zweite Reihe, bei der der Wulst von der Hemisphärenspitze zurückverlagert wird, während die frontale Zone von Neo- und Hyperstriatum ventrale sich als basale Front verbreitert und sich weit nach vorn ausdehnt. Diese Massenverschiebung wird als *basale Frontbildung* bezeichnet.

Fig. 3 zeigt in der oberen Reihe die verschiedenen Stufen der dorsalen Frontbildung. Von einem primären Hirntypus ausgehend wird in dieser Reihe der Wulst, welcher seitlich von einer Furche, der Vallecula, begrenzt ist, sukzessive verbreitert und über den ursprünglich die Spitze der Hemisphären markierenden Bulbus olfactorius hinaus, nach vorn verschoben.

Unten in Fig. 3 ist die Reihe der basalen Frontbildung dargestellt. Im Gegensatz zur dorsalen Frontbildung wird hier der basale Teil der Dorsalgebiete, das Hyperstriatum ventrale und das Neostriatum sukzessive nach vorne verschoben und verbreitert. Die Verbreiterung der basalen Front hat zur Folge, dass zwischen ihr und dem hinteren Teil der Hemisphäre eine laterale Furche auftritt.

Diese Umgestaltungen der dorsalen Gebiete wirken sich kompressiv auf die basalen Gebiete aus. In beiden Gestaltungsrichtungen werden die basalen Teile komprimiert und in der hohen Formstufe zum Teil umwachsen und ins innere der Hemisphäre abgedrängt.

Die experimentelle Prüfung dieser vogeltypischen Dorsalgebiete zeigt, dass vom Neostriatum und Hyperstriatum ventrale aus, also von jenem Bezirk aus, der in seiner frontalen Ausdehnung sehr stark variieren kann, sämtliche komplizierteren Leistungen des Tieres unter anderem wahrscheinlich das gesamte arttypische

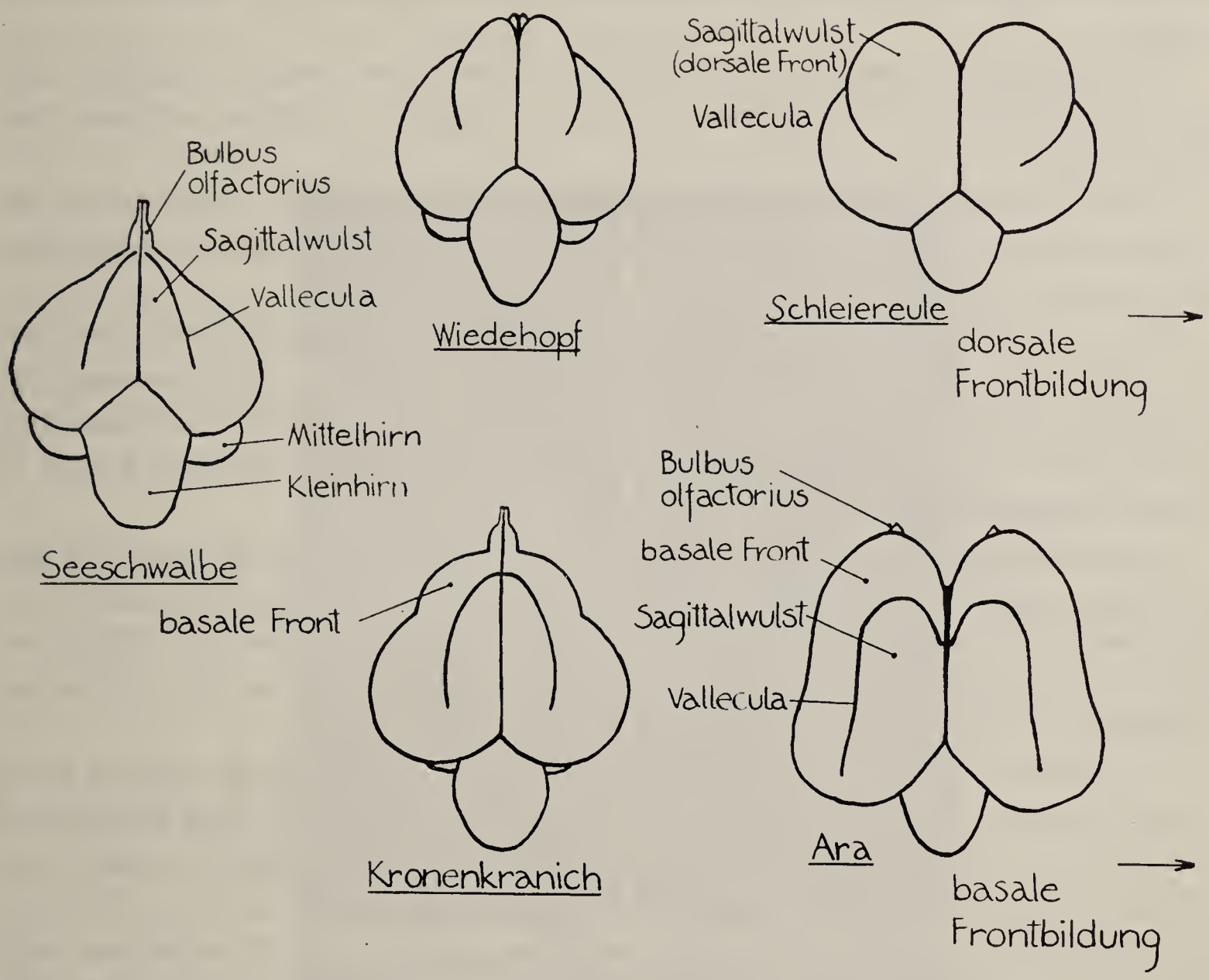

Fig. 3. Oberflächengestaltung der Vogelhemisphäre. Oben dorsale, unten basale Frontbildung. (Die Gehirne sind in dorsaler Aufsicht gezeichnet.)

Sozialverhalten, gesteuert wird. Das Tier verliert aber bei operativer Entfernung dieser Teile nicht nur die Fähigkeit zur Brutpflege oder Begattung, der Vogel wird allgemein apathischer, er zeigt weniger Spontanreaktionen, sein Fluchttrieb geht verloren. Diese Ausfallserscheinungen, die an einen Persönlichkeitsverlust erinnern, lassen vermuten, dass dieses Gebiet nicht nur eng umschriebenen Leistungen zugeordnet ist, sondern der gesamten Aktivität Sinn und Bedeutung in Form des individuellen Erlebens verleiht.

Noch mehr als das Neo-Hyperstriatum ventrale scheint das Sagittalwulstgebiet übergeordnetes Zentrum zu sein.

Die Tatsache, dass umschreibbare Ausfallserscheinungen bei Verletzung dieses Bezirkes nicht auftreten, deutet nicht auf ein funktionsloses Feld hin, sondern eher darauf, dass ein Assoziationsfeld vorliegt, ähnlich den Assoziationsfeldern bei den Säugetieren, bei welchen nach Verletzung ebenfalls keine umschriebenen sensorischen oder motorischen Störungen auftreten.

Wenn der Sagittalwulst innerhalb der Vogelklasse vergrössert wird, dann können

wir also nicht sagen, welche Leistungen eine Verbesserung erfuhren, d. h. wir können seinen Nutzen und Sinn im Vogelleben nicht in besonderen Einzelleistungen angeben.

Wir können aber feststellen, bei welchen Vögeln dieses Gebiet in geringer, mittlerer und hoher Formstufe entwickelt ist und so indirekte Schlüsse auf seine Aufgaben ziehen.

Auch die Funktion der basalen Gebiete ist im Einzelnen nur vage bekannt. Es bleibt auch hier nur der Weg des Vergleichs verschiedener basaler Frontstufen mit Eigenschaften der Lebensformen.

Bevor für die verschiedenen gestaltlichen Evolutionsstufen und Evolutionstypen des Vorderhirns auf eine systematische, oekologische oder verhaltensmässige Bedeutung geschlossen werden kann, muss abgeklärt werden, wie weit das Vorderhirn seine Gestalt autonom aufbaut und inwiefern auch von aussen wirkende Kräfte an seiner Gestaltung Anteil haben.

In erster Linie wäre hier an Schädelbau und Augengrösse zu denken. Der Bau des Spangenschädels wirkt sich, wie vergleichende Untersuchungen gezeigt haben, nicht aus auf die Konstruktion des Neurocraniums. Mit Ausnahme der Bildung von Muskelwiderlagern und der Bildung einer Schutzhülle um das Gehirn, sind andere Funktionen für das Neurocranium nicht nachzuweisen.

Der Schädel passt sich vollkommen der Form des Vorderhirns an und hat sicher keinen formgebenden Einfluss auf die Hemisphäre. Wäre der Schädel formbildend am Gehirnbau beteiligt, dann könnten wir die Tatsache nicht erkären, dass in den völlig unterschiedlich gebauten Schädeln von Schnepfe, Pelikan, Löffler und Papagei ein grundsätzlich ähnliches Vorderhirn vom Typus mit basaler Frontbildung liegt. Die Lage des Gehirns im Streck- und Knickschädel, etwa im Vergleich Kormoran-Waldkauz, hat ebenfalls keinen Einfluss auf die äussere Gestaltung des Gehirns. Streck- und Knickschädel bedeuten nur, dass das Gesamthirn eine Lageänderung aufweist. Entsprechendes gilt für die Augengrösse: Die Augengrösse kann höchstens für die Lage des Gehirns im Schädel verantwortlich gemacht werden, nicht aber für die Form des Vorderhirns.

Zusammenfassend sei festgestellt, dass eine Abhängigkeit der Vorderhirnform von Schädeltypus und Augengrösse nicht besteht. Das Vorderhirn entfaltet sich autonom, seine Grösse und Proportion muss weitgehend aus eigenem Gestaltungsgeschehen und aus seinen nervösen Aufgaben heraus verstanden werden.

Ist es nun möglich die verschiedenen Vorderhirntypen bestimmten Lebensformen, oekologischen oder anderen Typen zuzuordnen? Wird die Vorderhirngestalt aus der funktionellen Anpassung heraus verstanden oder ist sie nur aus der Art- oder verwandtschaftlichen Zugehörigkeit heraus zu verstehen, gewissermassen taxonomisches Merkmal?

Eine erste Antwort finden wir, wenn wir die Frage stellen, ob innerhalb einer Verwandtschaftsgruppe starke Unterschiede der Formevolutionsstufe eines Gestaltungstypus vorkommen können.

Als Bsp. mögen die Laro-Limicolae dienen. (Fig. 4). In dieser Ordnung haben Seeschwalbe und Möwe eine primäre Vorderhirngestalt; es gewinnt weder die basale, noch die dorsale Front eine besondere Ausdehnung.

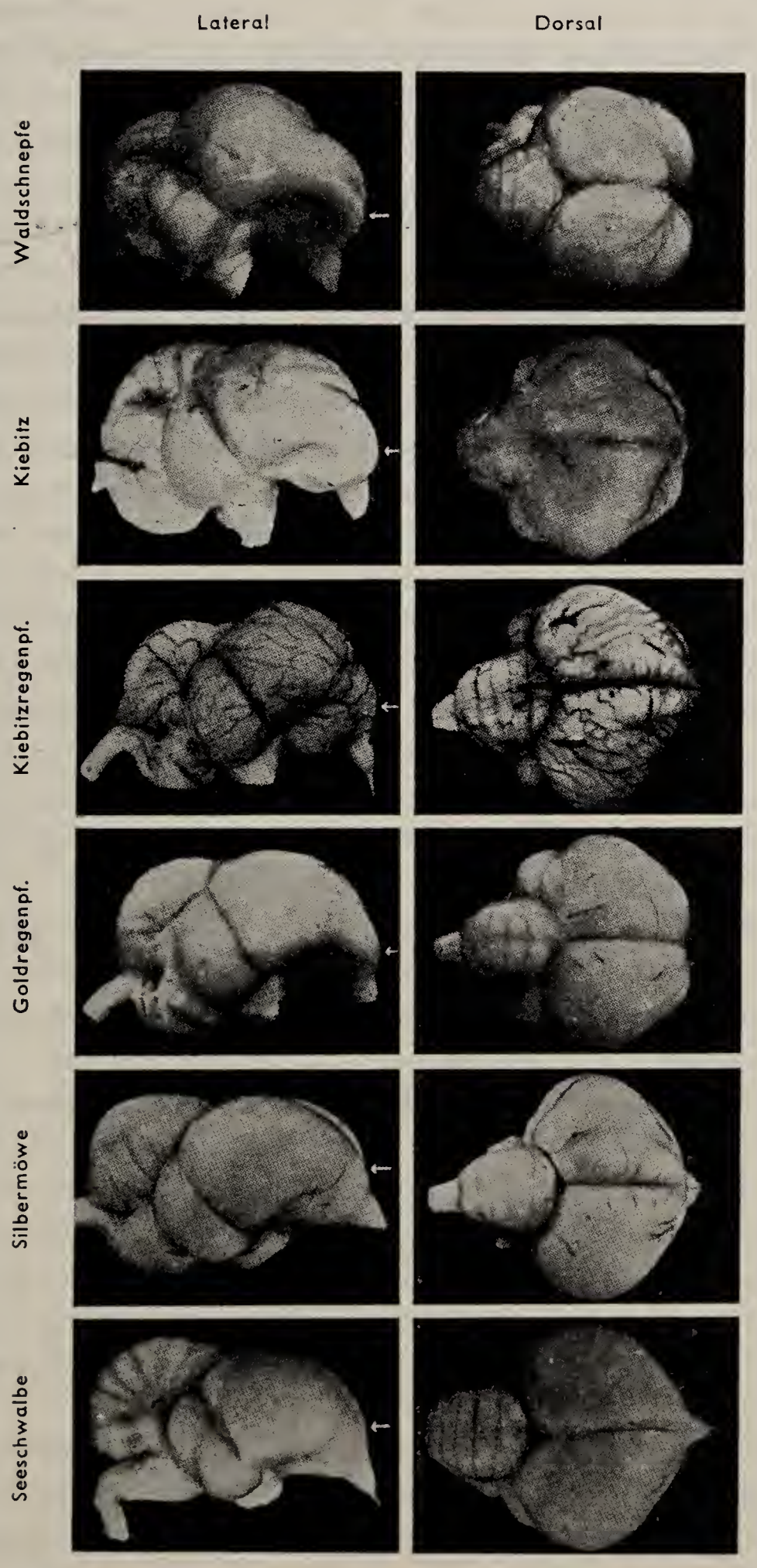

Fig. 4. Laro-Limicolae: Ausprägungsreihe der basalen Front. (Pfeil). Die Seeschwalbe, unten, weist eine niedrige, die Waldschnepfe, oben, eine hohe Formstufe auf.

Beim Goldregenpfeifer findet sich eine erste Andeutung einer basalen Front, beim Kiebitz hat die basale Front deutlich einen mittleren Formzustand erreicht, und bei den Schnepfen endlich ist die basale Front mächtig vorgewölbt.

Diese für den Systematiker sicher unerwartete Formevolution eines äusserlich nicht in Erscheinung tretenden Organs in einer relativ geschlossenen Verwandtschaftsgruppe bedeutet, dass solche Umformungen als Folge funktioneller Beanspruchung verstanden werden müssen.

Die Laro-Limicolae bilden nicht das einzige Bsp. einer solchen Formsukzession; für die Storchenvögel konnte eine ähnliche Gestaltungsreihe nachgewiesen werden.

Vergleicht man sämtliche untersuchten Arten, welche eine extrem ausgebildete basale Front aufweisen, es sind ausser den Schnepfen die Ibisse, die Entenvögel, der Flamingo, der Pelikan und die Papageien, dann erscheint diese Analogie des Hemisphärenbaues eine Parallele in der analog ausgeprägten Schnabelfunktion zu haben, nicht in einer entsprechenden Art und Weise der Funktion, aber in der entsprechend starken Innervation des Schnabelgebietes durch die Aeste des Trigeminus. Schaposchnikow hat bereits auf diese Beziehung Ausprägung der basalen Front des Vorderhirns und der vermehrten sensiblen Innervation des Schnabelgebietes hingewiesen.

Dieser Zusammenhang von basaler Frontbildung und Ausbau der Schnabelfunktion ist noch nicht stichhaltig nachgewiesen. Ich erwähne diesen sehr wahrscheinlichen Zusammenhang insbesondere darum, weil er zeigt, dass die Möglichkeit in Betracht gezogen werden muss, dass äussere Spezialisierungsmerkmale auch im höchsten Nervenzentrum repräsentiert sein können, resp. dass auch enger umschriebene Anpassungen an Milieubedingungen nur dann erfolgreich sind, wenn der sie steuernde Mechanismus ebenfalls ausgebaut wird.

Mit dieser Zuordnung Schnabelspezialisierung — basale Frontausprägung haben wir eine mehr oder weniger deutliche Beziehung erfasst. Ob noch andere, verborgenere Leistungen von diesem frontalen Integrationsgebiet aus gesteuert werden, bleibt eine offene Frage.

Im Gegensatz zur basalen Frontbildung ist die Vergrösserung des Sagittalwulstgebietes, die dorsale Frontbildung, nicht mit Spezialisierungsphänomenen in Zusammenhang zu bringen. Dass gerade eine so dynamische Gruppe wie die Passerinen ausnahmslos einen mächtigen und gut differenzierten Wulst besitzen und alle Arten der hohen Formstufe der dorsalen Frontbildung zuzuordnen sind, deutet nicht auf eine eng umschriebene somatische Funktion hin, sondern eher auf die Rolle des Wulstgebietes als Integrationsorgan bei der Anpassung an wechselnde Verhältnisse.

Die beiden Ordnungen, Eulen und Singvögel, welche die hohe Formstufe der dorsalen Frontbildung erreichen, zeigen innerhalb der Ordnung, von Familie zu Familie, keine Formevolution. Eine der basalen Frontbildung entsprechende Einteilung in niedrige, mittlere und hohe Formstufe ist also für die dorsale Frontbildung innerhalb der Verwandtschaftsgruppen nicht nachzuweisen.

Die Passerinenhemisphäre ist bei allen Arten von ähnlichem Gestaltungstypus. Spezialisierungen der Lebensweise, wie Nahrungs-Flugspezialisierung usw. finden keinen Ausdruck in den bisher erkannten Gestaltungsmerkmalen der Hemisphäre.

Die Hemisphäre der Passerinen ist im Gegensatz zum Vorderhirn der Laro-Limicolae ordnungstypisch gebaut.

Dagegen zeigt sich innerhalb der hohen Formstufe bei den Singvögeln wie bei den Eulen eine sukzessive Ausprägung und Skulpturierung des Sagittalwulstes, welche der Körpergrössensteigerung parallel geht.

Fig. 5 zeigt einen solchen Gestaltungsunterschied verschieden schwerer Formen am Bsp. der Eulen.

Die kleinste Form, die Zwergohreule hat den am schwächsten, der Steinkauz (in der Zeichnung nicht dargestellt) von mittlerem Gewicht einen gut ausgeprägten und die schwerste Form, die Schleiereule, den auffälligsten Sagittalwulst. Ähnliches gilt für die Passerinen, wo ebenfalls die grössten Vertreter, die Corviden, den auffälligsten Sagittalwulst aufweisen.

Welche Bedeutung die proportionale Vergrösserung des Wulstes in der Eulenreihe hat, ist schwer zu entscheiden; es könnte sein, dass hier allein die Vergrösserung der absoluten Körpermasse diese vermehrte Skulpturierung bedingt. Ob mit der Vergrösserung des Wulstes auch eine höhere Verhaltensstufe erreicht wird, erlaube ich mir nicht zu entscheiden.

Wenn man hingegen den Kolkraben mit einer kleinen Passerinenform vergleicht,

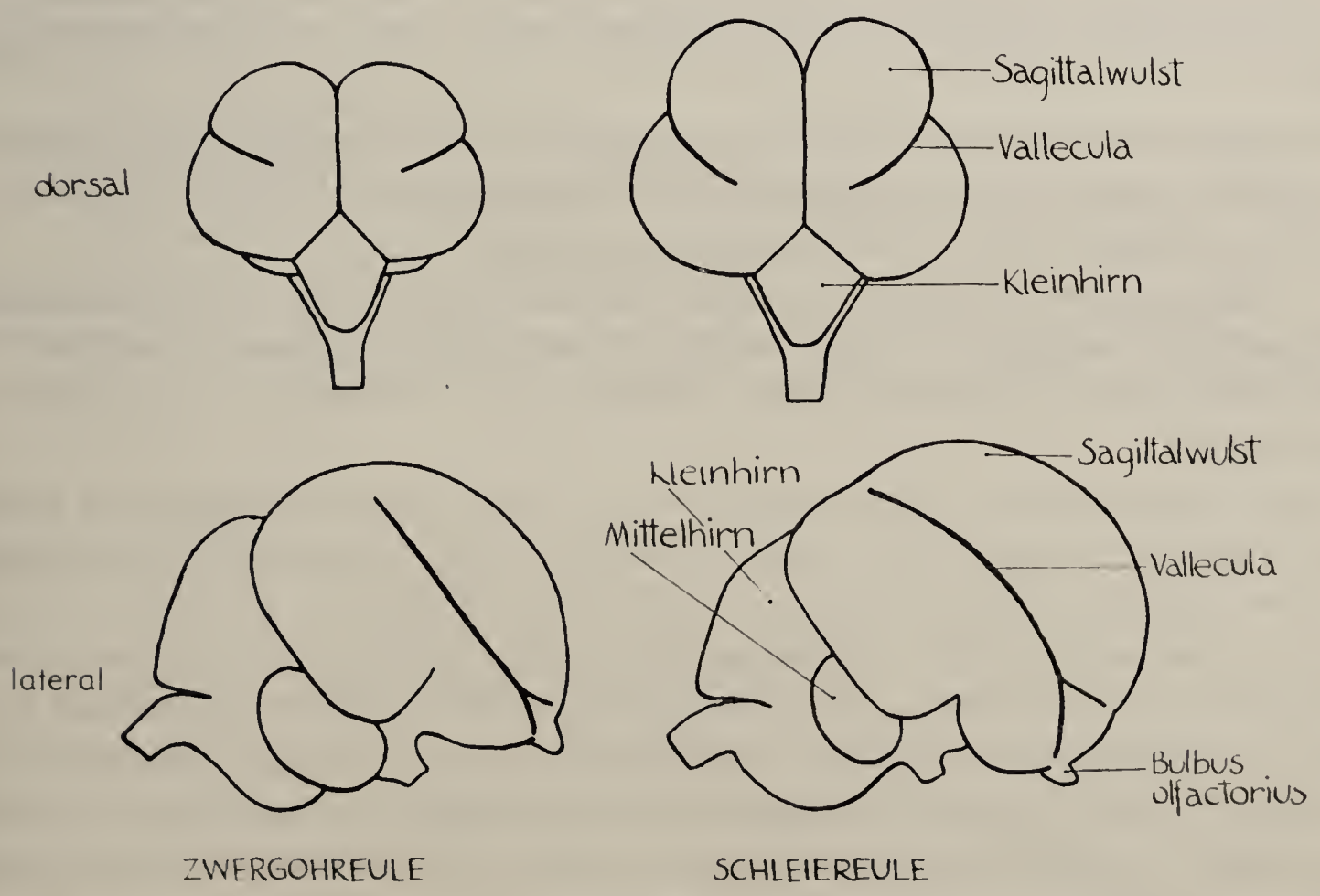

Fig. 5. Skulpturausprägung bei zunehmender Körpergrösse. Bei der nur 90 g schweren Zwergohreule ist der Sagittalwulst bedeutend kleiner, als bei der 300 g schweren Schleiereule.

z. B. dem Fliegenschnäpper, dann scheinen hier doch zwei verschiedene psychische Stufen vorzuliegen.

Man darf somit annehmen, dass die Ausprägung der Skulptur, resp. die rel. Grössensteigerung des Wulstes wohl körpergrössenabhängig ist, dass das grössere Gehirn aber gleichzeitig auch eine Steigerung der Integrationsleistung bedeutet. Nicht nur bei der hochevoluierten Gruppe der Passerinen scheint eine solche Beziehung von Körpergrössensteigerung, Skulpturierung der Hemisphäre und Integrationstätigkeit zu bestehen, auch bei den Papageien, welche basale Frontbildung aufweisen, ist eine ähnliche Sukzession von kleinen Formen bis zur grössten Form, dem Ara, aufzuweisen.

Diese auffällige Tatsache, dass Ara und Kolkrabe, die schwersten Vertreter der beiden höchstevoluierten Vogelordnungen, jeder in seiner Gestaltungsrichtung das differenzierteste und skulpturierteste Vorderhirn unter den Vögeln überhaupt aufweisen, scheint mit ganz generell dafür zu sprechen, dass nicht nur die Vergrösserung des Wulstes, sondern die Vergrösserung des Vorderhirns überhaupt (welche in dieser Skulpturierung sichtbar wird) im Verein mit der zellulären Differenzierung, im Sinne der Intensivierung der Schichtstruktur, ein wesentliches Kriterium der morphologischen Evolution und ein Indizium der funktionellen Anpassung ist.

Vergleichen wir abschliessend noch einmal die aufgewiesenen Zusammenhänge, dann stellen wir am Beispiel der Laro-Limicolen einerseits fest, dass der Anpassungstypus im Vorderhirnbau morphologische Entsprechungen finden kann, andererseits stellen wir am Beispiel der Eulen und Singvögel fest, dass die Hemisphären in grossen Zügen einander durchgehend ähnlich, ordnungstypisch sind, dass also hier die unterschiedlichen Lebensformen keine auffällige Repräsentation in der Hemisphäre finden.

Hingegen kann bei den Passerinen eine andere Gesetzmässigkeit aufgezeigt werden, nämlich die, dass die Ausprägung des ordnungstypischen Vorderhirns der Körpergrössenzunahme und Verhaltensstufe parallel geht.

Als allgemeinstes Ergebnis sei noch einmal erwähnt, das die evoluiertesten und indexhöchsten Gruppen wie Eulen, Singvögel und Papageien parallel zu ihrer Gesamtevolution auch die höchste Differenzierungs- und Gestaltstufe des Vorderhirns erreicht haben.

Wenn bis vor kurzem das Vorderhirn der Vögel formal als weitgehend gleichförmig betrachtet wurde, als ein Organ, welches für die vergleichende Betrachtung nur Unwesentliches beitragen kann, so hoffe ich im Gegensatz zu dieser Meinung gezeigt zu haben, dass die Vogelhemisphäre stark variabel ist, und dass Gesetzmässigkeiten der Gestaltung und Differenzierung in Wirklichkeit nachweisbar sind. Wenn der vorläufige Beitrag zum Adaptationsproblem auch sehr bescheiden ist, so hoffe ich doch, dass die vergleichende morphologische Untersuchung weitere, wenn möglich kombinierte Untersuchungen durch Verhaltensforscher, Physiologen, Ökologen und Morphologen anzuregen vermag.

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Evolution in the Diving Birds

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The conquest of land by the early tetrapods is a classic story of evolution. This development of terrestrial lines from aquatic ones has been a relatively rare phenomenon in the history of the earth; among the chordates, for example, it appears to have occurred but once. On the other hand, many terrestrial lines have given rise to aquatic forms. Among the reptiles alone, at least six major groups have been aquatic or have included aquatic members. The mammals, with a much shorter history, also contain an impressive number of aquatic groups.

The evolution of aquatic lines of birds started early and has continued through many geologic periods. The highly specialized toothed divers, the Hesperornithes, flourished with the last of the dinosaurs in the late Cretaceous, and by this early time, the superficially gull-like Ichthyornithes and members of at least three aquatic orders, the Anseriformes, the Phoenicopteriformes, and the Pelecaniformes had made their appearance. It is not unlikely that other lines of aquatic birds were also found this early, but so far we have no fossil evidence of them.

At this point, it should be brought out that *Hesperornis* is the only bird of Cretaceous age which we know had teeth. GREGORY (1952) has presented convincing evidence that the toothed jaws formerly assigned to *Ichthyornis* were probably those of mosasaurs. If this is so, we may look on the teeth of *Hesperornis* as structures of high adaptive value in the capturing and holding of fish — structures which were retained in this group after they had been lost by the main line of avian evolution.

The avian body is first and foremost adapted for flight. Modifications for an aquatic existence have been superimposed on this plan with varying degrees of success. Among the Amniotes, viviparity is a requisite for a completely aquatic existence. No bird has achieved viviparity, so even the most aquatic of birds must return to the land, or at least must make a floating nest, in the breeding season. The stiffening of the trunk skeleton and the horizontal plane of the tail have prevented the development of these parts of the body as swimming organs. Hence only the wings and the feet have been modified for locomotion in the water. Buoyancy, so important in flight, is a disadvantage in diving and has been circumvented in various ways. In

the loons (Gier, 1952) and presumably in other groups of diving birds, the air sacs have been reduced in size and the bones are little if at all pneumatic. Diving birds are further able to increase their effective specific gravity by keeping their feathers appressed to the body while under water, thereby greatly reducing the amount of air trapped between the plumage and the skin.

Diving birds can be divided into those which use their wings and those which use their feet for swimming under water. The scoters appear at first sight to be an exception; but according to Brooks (1945), the partly opened wings with the strongly extended alulas are held virtually motionless while the birds are under water. Some shearwaters (e. g. *Puffinus griseus* and *P. tenuirostris)* are exceptional in that both their wings and their legs show modifications for underwater use (Kuroda, 1954), but these birds are by no means as strongly modified for this purpose as are other diving birds. Loons may use their wings as well as their feet under water when pressed or wounded (Townsend, 1924), but normally they, the grebes, and the extinct Hesperornithes are or were foot-propelled divers; and the alcids, the diving petrels, and the penguins are wing-propelled divers. These six groups of birds are the most highly specialized for submarine locomotion and will therefore be the subject of most of this discussion.

In his important paper on the fossil penguins, Simpson (1946) brought out the idea of quantum evolution, using the wing-propelled divers as an example. In the case of these birds, there are three »quanta» or adaptive stages (Figure 1); the first,

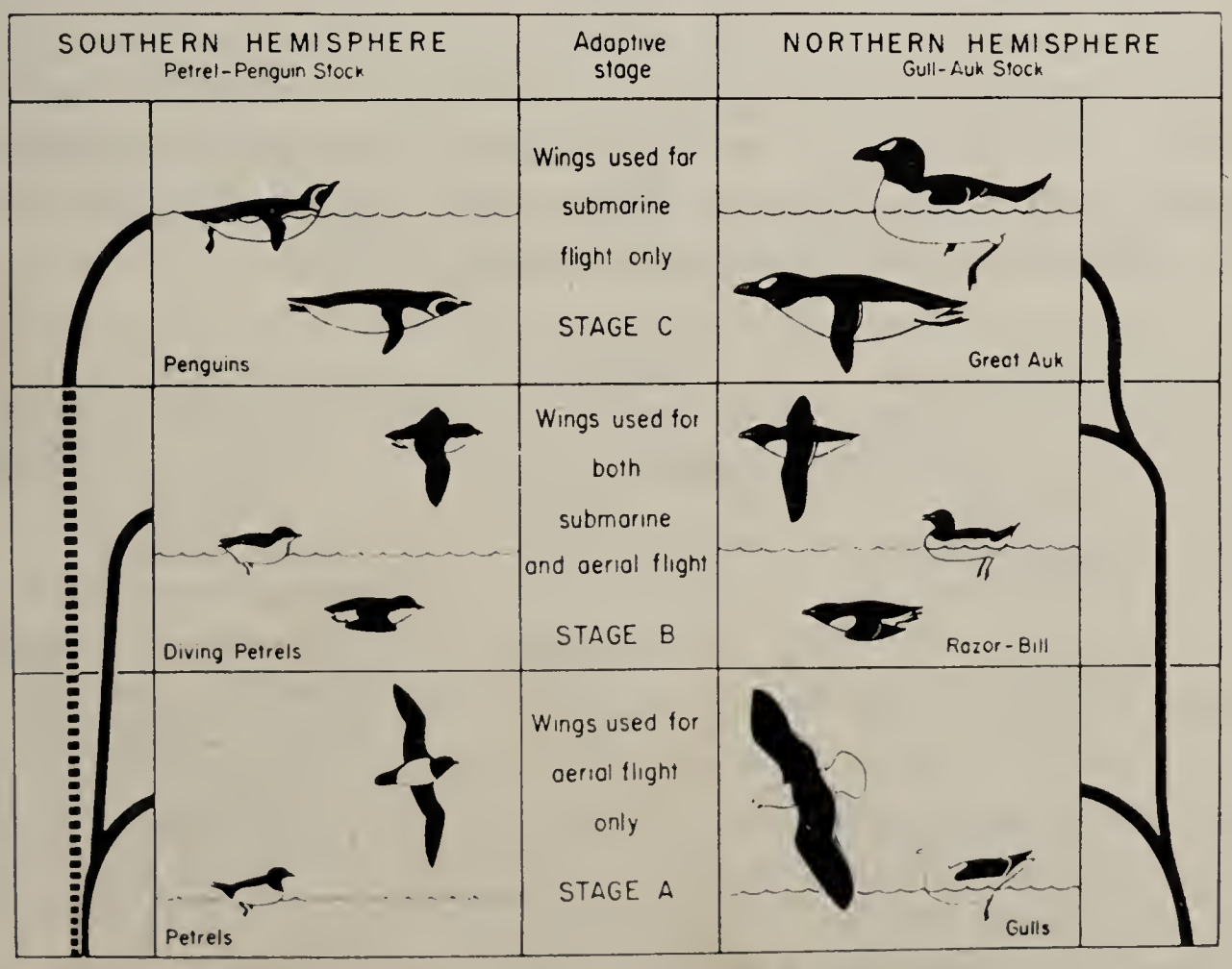

Fig. 1. Adaptive stages or quanta in the evolution of wing-propelled divers.

in which the wings are used for aerial flight only; the second in which they are used for both aerial and submarine flight; and the third, in which they are used only for submarine flight. SIMPSON believes, and I think correctly, that evolution proceeds rapidly from one quantum or stage to the next whereas it proceeds more slowly within a quantum.

The wing-propelled divers are marine and are predominantly pelagic forms. Why these birds have so to speak »taken over» the marine habitat and the foot-propelled divers have adopted the fresh-water and littoral habitats remains to be answered. A possible explanation is that upright aquatic vegetation, such as is commonly found in fresh-water habitats, must impede wing-propelled divers to a much greater extent than foot-propelled ones.

The geographic distribution of the wing-propelled divers is an illustration of convergent evolution on a regional basis. The auks, presumably derived from gull-like ancestors are widely distributed in the Northern Hemisphere; whereas in the Southern Hemisphere, we find the diving petrels and the penguins, which were probably both derived from procellariiform stocks. On the other hand, the segregation between the gulls and the petrels is primarily an ecological one, the former being predominantly littoral forms and the latter, pelagic ones; both occurring in both hemispheres.

If we divide the wing-propelled divers into groups on the basis of size we find a considerable difference between the forms found in the two hemispheres (Table 1). Large birds of the »penguin» stage (C) are absent in the north, and medium-sized birds of the »auk» stage (B) are absent in the south. Large birds in the alcid stage (B) are a virtual impossibility. The wings of these birds represent a »compromise» adaptation, on the one hand being subjected to selection favoring large wings for aerial flight and on the other hand to selection favoring small wings for underwater use. While under water, alcids reduce the effective area of their wings and increase the strength of these structures by keeping them partly folded.

TABLE 1

*Distribution and Size Range of Wing-propelled Diving Birds in Different Adaptive Stages**

	Southern Hemisphere		Northern Hemisphere	
Size Range in inches)	Group	Stage	Group	Stage
6 to 11	Diving petrels	B	Dovekie (Atlantic)	B
			Auklets, Murrelets (Pacific)	B
12 to 20	Penguins (3 species)	C	Razor-bill, Murres, Puffins, Guillemots	B
			† Lucas Auk	C
24 to 32	Penguins (most species)	C	† Great Auk	C
36 to 48	Penguins (2 species)	C		
50 to 64	† »Giant» Penguins	C		

* See Figure 1 for definitions of stages.

† Extinct forms.

To understand how birds possessing this »compromise» adaptation are limited in both the maximum and minimum sizes which they can, in an evolutionary sense, attain, we must consider certain aspects of the surface: volume ratio. If we remember that surface area varies with the square, and volume (or weight) with the cube, of linear proportions, it is apparent that in two birds of similar shape, the larger will have the greater wing loading. In order to keep in the air, the larger bird must have a greater minimum flight speed (the actual figure is length to the one-half power). To achieve this greater flight speed, the bird must have proportionately larger pectoral muscles. This relationship has been shown in three hawks of the genus *Accipiter* (Storer, 1954). In other words, large birds must have either proportionally larger wings and/or larger pectoral muscles than smaller birds. In the case of the alcids which possess the »compromise» adaptation, the maximum size obtainable is limited by the maximum size of wing which, partly folded, can be effectively used as a paddle and by a maximum proportion of muscle. The maximum size obtainable by flying alcids appears to be near that of the murres *(Uria)* or the Razor-bill *(Alca)*.

When the wings are used for propulsion under water, buoyancy is not a significant factor and the size of the paddle (that is, the wing) needed to push the bird through the water is proportional to the cross-sectional area of the bird. As both of these are areal functions varying as the square of linear proportions, birds which have lost the power of aerial flight (stage C) are not limited in maximum size by the surface: volume ratio, and we find such relatively large species as the Great Auk and the large penguins among the birds of this evolutionary stage.

Wing area also appears to limit the minimum size attainable by birds with the »compromise» adaptation. As alcids become smaller (in an evolutionary sense), the relative difference between the optimum sizes for flight in the air and in water becomes less. As a general rule, alcids molt all their remiges at once, and during the period of growth of the new flight feathers, the large flying alcids still use their wings effectively under water. In the case of very small birds of the alcid type, the relatively small wing needed for aerial flight, when folded becomes more nearly the optimal size for use under water. Reduction in the size of the wing through the simultaneous loss of the remiges might prove too great for effective use under water. This theory is borne out by the fact that while the Dovekie and the murrelets molt their remiges simultaneously, the smallest alcids, *Aethia pygmaea* (Stejneger, 1885) and *Ae. pusilla*, molt them one at a time like most birds.

Apparently the Great Auk also molted its remiges one at a time. A specimen in the University Museum, Copenhagen, shows the beginning of the wing molt: on the right wing, a pin feather is to be seen near the middle of the series of primaries; and on the left wing, one primary (the sixth or seventh counting from the outermost) appears new whereas the rest of the primaries are faded and badly worn. That the Great Auk should have molted in this manner is not surprising. The wing of this species was presumably near the optimum size for use under water, hence the simul-

taneous loss of all the remiges would presumably have been disadvantageous in an adaptive sense.

The alcids are an ancient group and have undergone adaptive radiation in both feeding and nesting habits (Figure 2). As regards feeding, the guillemots or teisties *(Cepphus)* are primarily bottom feeders and are littoral in their distribution. The other groups feed primarily on pelagic organisms, the Dovekie *(Plautus)* and the small auklets *(Aethiini)* taking crustaceans and the larger forms, fish. The food of many species of alcids is not well known, and the careful working out of this radiation in feeding habits would be a most promising study.

The available nesting sites for sea birds are relatively few, and with the wing modified as the principal locomotor organ in the water as well as in the air, the hind limb has been »available» so to speak for modifications enabling the birds to occupy different types of nesting sites (Storer, 1945). This radiation is most evident in the

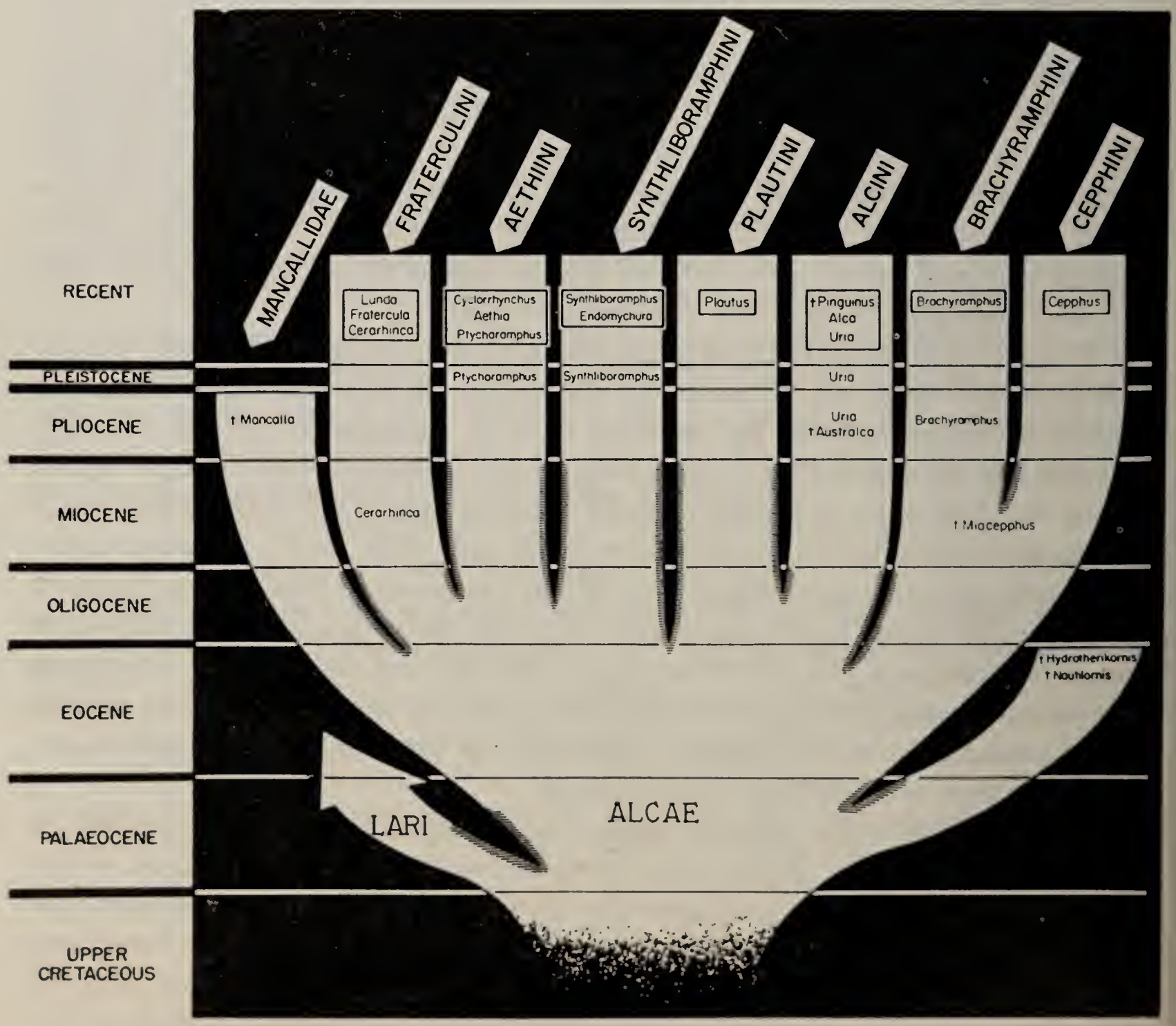

Fig. 2. A phylogenetic tree of the auks.

colonial forms. The Dovekie and auklets nest among boulders and in natural crevices, the puffins (including *Cerorhinca*) have stout feet, well adapted for digging nest burrows. The murres colonize flat ledges, resting the single egg on the tarsi as they incubate. The Black and Pigeon Guillemots, which on the average nest in smaller groups than other alcids, utilize the widest variety of nest sites. Some use natural crevices in cliffs, others nest under boulders or in thick grass, and still others dig burrows like the puffins. The significance of the short, wide tarsi of the *Brachyramphini* (Marbled and Kittlitz murrelets) remains to be demonstrated. The latter species nests in the open above timber line; the former's nesting habits are unknown. The long, flattened tarsi of the *Synthliboramphini* (murrelets of the genera *Synthliboramphus* and *Endomychura*) indicate that these birds depend more on the feet for swimming under water (at least when the birds are young) than do other alcids. The downy young of these two genera go to sea at the age of approximately two days, at which time their feet are nearly as large as those of their parents. The young of all other alcids do not take to the water until their wings are sufficiently large for use in swimming.

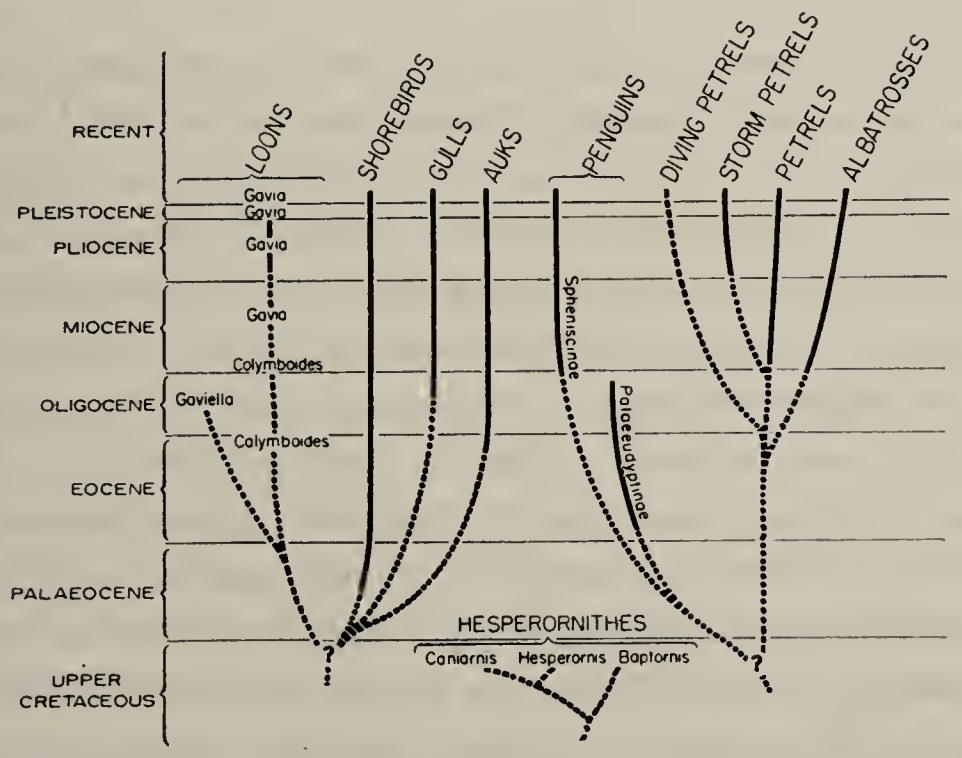

Fig. 3. Phylogenetic trees of the toothed divers, loons, charadriiform birds, penguins, and petrels.

Of the wing-propelled divers, the penguins are by far the most specialized (Figure 3). The fossil record sheds little light on their ancestry — the earliest known fossil penguins were nearly as highly specialized as are modern ones. Simpson (1946) has pointed out skull characters which indicate a relationship with the petrels, and it is not unlikely that the two groups had a common ancestry.

The penguin's flipper seems so unlike the wing of a flying bird that at first sight one is tempted to speculate that the penguins' ancestral stock never went through a flying stage. However, when the wings of a gull, a Razor-billed Auk, a Great Auk, a Lucas Auk *(Mancalla)*, and a penguin are compared (Figure 4), it is easy to imagine the stages through which the penguin flipper passed to reach its present condition.

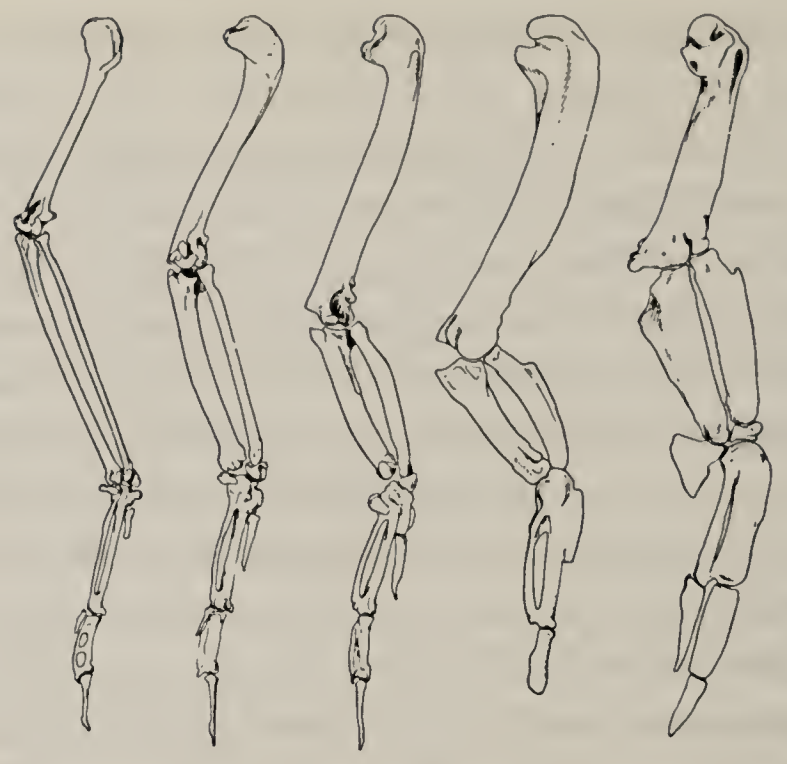

Fig. 4. Left to right, wing skeletons of a gull *(Larus)*, Razor-billed Auk *(Alca)*, Great Auk *(Pinguinus)*, Lucas Auk *(Mancalla)*, and penguin *(Spheniscus)*, showing adaptive stages similar to those through which the penguin flipper evolved.

The foot-propelled divers present a different set of problems. Quantum evolution is not evident in these birds; instead, the modification of the hind limb for use in diving has probably been gradual. Also in contrast with the wing-propelled diving birds, the Recent foot-propelled divers are birds of fresh water or of estuarine or littoral situations. The Cretaceous Hesperornithes, however, were birds of shallow seas.

The tremendous development of the hind limb musculature in foot-propelled divers, is associated with a reduction in the relative size of other structures. In birds of this type which lose the power of flight, the wings become degenerate, as for example, those of the Hesperornithes, the flightless grebe *(Centropelma)*, and the Galapagos Cormorant *(Nannopterum)*. Among the species which can fly, several perform long migrations. Although the wing morphology of loons and grebes remains to be studied in detail, one might expect to find in these birds adaptations for maintaining direct, rapid flight with a minimum weight of wing musculature (Storer, 1958).

In collecting data on weight and wing area on Pied-billed Grebes *(Podilymbus podiceps)*, I have found little variation in wing area; but I have found a tremendous variation (over 100 per cent) in body weight and, hence, in wing loading. More surprising than this is the variation in weight of the pectoral muscle. In males taken in October and November, the weight of *M. pectoralis* plus that of *M. supracoracoideus* on one side varied from 12.2 to 31.9 grams (19 measured). Most of these birds, including the two extreme individuals, were birds of the year, and it is likely that some of this variation is due to the fact that the muscles associated with flight are the last to develop in these birds. However, one adult with much subcutaneous fat had pectoral muscles weighing 19.5 grams, less than $^{2}/_{3}$ that of the extreme of the young birds.

It may be that these birds, which rarely fly except on migration, not only build up tremendous reserves of fat but also greatly increase the mass of their flight muscles prior to migration. The muscle samples have not as yet been analyzed for fat content, but superficial examination showed no obvious deposits of fat within them.

The loons, the grebes, and the Hesperornithes all show a remarkable resemblance in the general aspects of body form and the development of the hind limb. In all, the body is (or was) broad and thus very stable when on the surface. The extra width of body is provided by the hind limb. The pelvis is very narrow, and the short, stout femora have a double, hinge-like articulation with the acetabulum and the antitrochanter. The femora and the tibiotarsi lie nearly in the frontal plane passing through the acetabula, and all but the distal ends of the tibiotarsi lie within the main body mass. Both stabilizing breadth and »streamlining» are provided by this arrangement, which also results in placing the feet near the posterior end of the body. Having the feet so far aft, coupled with a considerable ability to rotate the tibiotarsus, makes it possible for these birds to move their feet above, below, or on a level with the body when under water. Hence steering can be accomplished on the propulsive strokes and thus with a minimal loss of energy. The large cnemial crest and the laterally compressed tarsus are two other striking morphological characters found in the foot-propelled divers.

The fossil loon *Colymboides minutus* shows well a stage in the evolution of the highly specialized Recent loons (Storer, 1956). It was a small species, approximately the size of a small grebe. In Figure 5, the three elements of this fossil are shown the same size as those of a Common Loon *(Gavia immer)* to emphasize the differences in proportion. The relatively wider synsacrum, the shorter cnemial crest on the tibiotarsus, and the less compressed tarsometatarsus are evident on the fossil.

The *Hesperornithes*, the loons, and the grebes are outstanding examples of convergent evolution. In fact, I doubt that they even had a common swimming ancestor. Looking at the fossil record (Figure 3), we find that the Hesperornithes became extinct long before even the most primitive loons appeared. Our knowledge of the grebes gives no clues as to the ancestry of the group. The earliest fossil known being of questionable age (probably Oligocene) and attributable to the modern genus *Podiceps*.

Three of the major morphological differences indicative of the convergent evolution of the foot-propelled divers are in the cnemial crest, the pelvic musculature, and the structure of the foot. In *Hesperornis* and its relatives, the enormous patella formed the cnemial crest; in the loons this crest is formed by a projection of the tibia; and in the grebes, the patella and the tibia together form the crest. The differences in the arrangement of the pelvic musculature in loons and grebes are hardly less striking than the differences in the cnemial crest. In Figure 6 are shown the areas of attachment of some of the pelvic muscles in a grebe *(Podilymbus)* and a loon *(Gavia)*. The attachments of homologous muscles in the two species are shown in

Fig. 5. Tibiotarsi (above), tarsometatarsi (below, left), and synsacra (below, right) of (A) an early fossil loon *(Colymboides minutus)* and (B) a Common Loon *(Gavia immer)*. The bones of the small fossil species and the large Recent one are shown the same length to emphasize the differences in proportions.

the same type of shading. The three arrows indicate attachments of three muscles which are present in the loons but absent in the grebes.

Stolpe (1935) has well described the action of the toe joints in loons and grebes. The former flex the toes without rotating them immediately prior to the recovery stroke in swimming; the grebes however, rotate the toes as they flex them so that the toes are brought forward lateral side first with the long mesial lobes trailing and the shorter lateral lobes folded against the under side of the toe. The foot of *Hesperornis* shows several unique features. The fourth (or outer) toe is by far the largest and heaviest, and the trochlea for it on the tarsometarsus is not only the largest but the most anterior of the trochleae. The three proximal phalanges of the fourth toe are very heavy and are not flattened as are those of the other toes. They have an odd »ball and flange» type of articulation which shows that the toe was rotated, like those of grebes, between the recovery and power strokes. The undersides of these three

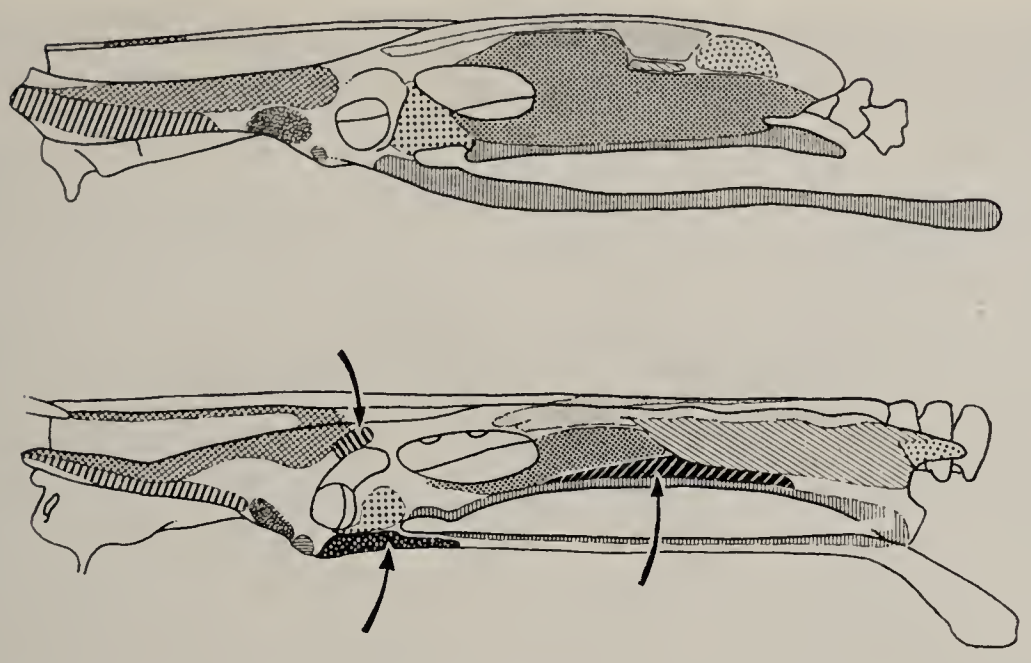

Fig. 6. Areas of attachment of some of the pelvic muscles of a grebe and of a loon. Above, the Pied-billed Grebe *(Podilymbus podiceps)*. Below, the Common Loon *(Gavia immer)*. Attachments of corresponding muscles are shown in similar shading; arrows point to attachments of three muscles found in loons but not in grebes. (Illustration of *Gavia* after WILCOX, 1952).

phalanges are deeply excavated as though for the attachment of stiffening for swimming lobes or for webbing. The phalanges for the other toes are weaker and are laterally compressed, especially those of the third toe. MARSH, in his monograph of the *Odontornithes* (1880), stated that the toes of *Hesperornis* must have been webbed because of the relative weakness of the third toe; STOLPE, on the other hand *(op. cit.)*, claimed that the joints of the fourth toe which rotate the phalanges as the toe is flexed make sense only if the toe is lobed rather than webbed. Each, I think, is partly correct. The relative weakness of all toes but the fourth, is good evidence for the presense of webs — and it must be remembered that even the grebes, with their highly developed swimming lobes, have partially webbed feet. On the other hand, the rotation of the fourth toe and the excavations on the underside of the phalanges indicate the presence of a firmly anchored lobe or stiffening device for the webs. A more thorough study of the foot of *Hesperornis* would almost certainly prove worth while. There is considerable excellent material available, and it is not impossible that an impression of the foot may still be unearthed.

The *Bathornithidae*, contemporaries of *Hesperornis* and therefore not ancestral to that genus, show some characters which were almost certainly shared by the ancestors of *Hesperornis*. *Bathornis* was smaller than *Hesperornis*. On the tarsometatarsus, the trochlea for the fourth toe was placed nearly on a level with that for the third toe, and the two outer toes were more nearly the same size. While flightless, *Bathornis* had a less degenerate wing than *Hesperornis*. It has even been suggested that *Bathornis* used its wing in submarine flight; the weakness of the wing bones, however, makes this seem unlikely.

Although the known fossil record of the grebes tells us nothing of the origin of the family, the group is sufficiently large and diverse for us to study evolution at the generic and specific levels. At Michigan we have recently initiated a long-term study

of the comparative anatomy and behavior of the grebes. Already we have found evidence of considerable adaptive radiation within this well-defined family. Even the hind limb, which one might expect to be rather similar in structure throughout the group, shows significant differences from one genus (or subgenus) to another.

Of the shank muscles, *M. flexor perforatus digiti II* was not found in *Podiceps caspicus* by HUDSON (1937). However, we have found it present and well developed in *Podilymbus*. The tendon for this muscle passes through a separate bony canal in the hypotarsus, hence the presence or absence of the canal may be taken as good evidence for the presence or absence of the muscle in grebes. Checking skeletons of the Northern Hemisphere species of grebes we found evidence of this muscle only in the two species of Pied-bill *(Podilymbus podiceps* and *P. gigas)* and in the Dabchick *(Poliocephalus ruficollis)*. Its absence in *Poliocephalus dominicus* suggests that the species placed by PETERS (1931) in *Policephalus* may not form a natural group.

The Pied-billed Grebes also differs from other grebes in the outline of the foot (Figure 7). Although the areas of the two feet illustrated are nearly the same, owing to the longer toes and the reduced webbing of the foot of *Podiceps auritus*, the center of resistance lies farther distad, and other factors being equal, greater speed can be developed with a foot of this shape than with one like that of *Podilymbus*.

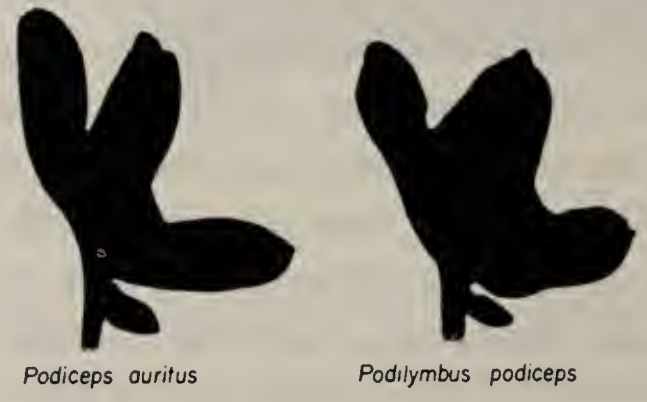

Fig. 7. Outline of the foot of a Horned Grebe *(Podiceps auritus)* and of a Pied-billed Grebe *(Podilymbus podiceps)*.

At least in North America, the major radiation in grebes is in their feeding habits (WETMORE, 1924). The two small species of *Podiceps*, *P. auritus* and *P. caspicus*, feed primarily on small invertebrates during the nesting season; the former nests on small bodies of water and the latter in large colonies on lakes. In winter *caspicus* is a bottom feeder, again taking mostly invertebrates whereas *auritus* takes more fish. The larger *Podiceps grisegena* resembles *auritus* in general habits, but inhabits larger bodies of water and takes more fish during the breeding season.

The heavy bill of *Podilymbus* and its correspondingly heavy jaw musculature appear to be adaptations for feeding on the crayfish and other crustaceans which form a relatively high percentage of its diet. The conformation of the side of the skull (Figure 8) in the Western Grebe *(Aechmophorus)* in comparison with *Podilymbus* and the Great Crested Grebe *(Podiceps cristatus)* is indicative of important differ-

Fig. 8. Skulls of grebes, showing differences in bill form and in the areas of attachment of jaw muscles. Top to bottom, *Aechmophorus occidentalis* male and female, *Podiceps cristatus*, and *Podilymbus podiceps*.

ences in the attachment of the jaw muscles — another problem in functional anatomy which we hope to study.

The Western Grebe *(Aechmophorus)* appears unique among the grebes in that it spears the fish on which it feeds. LAWRENCE (1950) has illustrated fish which these birds had speared, yet no one appears to have worked out the associated anatomical mechanism. The corresponding adaptations in the Anhinga, which include the consolidation of many smaller neck muscles into major dorsal and ventral ones and the pulley for the tendon of the dorsal muscle are well known (BOAS, 1929). In the grebes, the myology has yet to be worked out, but the elongation of the vertebrae in *Aechmophorus* and the large chevron-shaped processes on the posterior vertebrae (Figure 9) indicate a similar adaptation. This specialization of the vertebrae is not found in the Great Grebe *(Podiceps major)* of South America — strong evidence for the unique position of *Aechmophorus occidentalis* and for following WETMORE and PARKES (1954) in placing the Great Grebe in the genus *Podiceps*.

Fig. 9. Cervical vertebrae of *Aechmophorus occidentalis* and the smaller *Podilymbus podiceps;* above, in dorsal view; below in lateral view.

Two particularly interesting problems of sibling species remain to be studied. There appears to have been a triple invasion of Madagascar by the Dab-chick *(Poliocephalus)*, as two endemic species *(P. pelzelni* and *P. rufolarvatus)* and the African race of the widespread *P. ruficollis* all occur there. The second case is of the widespread South American species *Podiceps occipitalis* which occurs with an endemic species *P. taczanowskii* on Lake Junin in Peru. These forms are nearly identical in plumage, but the latter is larger and has a relatively larger bill.

Finally, I should mention behavior and its evolution. The grebes possess complex, stereotyped behavior which is unusually well adapted for analysis. The basic studies of Huxley (1914) and Simmons (1955) on the Great Crested Grebe form an excellent basis for comparing the behavior of other species. While our studies are still in the preliminary stages, we can already make several interesting points. As might be expected, the solitary or territorial species possess certain behaviorisms associated with threat or territorial defence which appear to be lacking in such colonial-nesting species as the Western Grebe *(Aechmophorus occidentalis)* and the Black-necked Grebe *(Podiceps caspicus)*. In the Great Crested and Red-necked Grebes *(P. cristatus* and *P. grisegena)* »token diving» is commonly used as threat, and in the latter species and in *P. auritus*, there is a ceremony in which the members of a pair swim side-by-side, with the feathers of the neck ruffed out, and call together. This duetting

sometimes appears to be used as a »song» and at others (at least in *P. auritus*) as a »triumph» ceremony. (A pair of Great Crested Grebes often swims side-by-side, but the neck feathers are not ruffed out and the birds do not call at this time.)

In contrast, the highly colonial Western Grebe has a unique ceremony. It starts with two (or occasionally as many as seven) birds face to face on the water calling in an apparently aggressive manner. The birds then rise and dash across the water, dive and rise again, this time moving slowly forward shaking their heads from side to side. The meaning of this ceremony has yet to be proved. Unlike the breeding-season displays of other grebes, it is not confined to the pre-incubation period but can be observed later in the breeding cycle. It is performed away from the nest sites, and although most frequently performed by a male and a female, two males or two females may also perform it (R. W. Nero, personal communication). This ceremony may prove to be a ritualized aggressive display valuable in an adaptive sense as a means of reducing actual combat within nesting colonies. This is another of the many points which we hope our future studies will clarify.

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Vogelkundliche Arbeit im engen Raum auf weite Sicht

WERNER SUNKEL

Tann (Rhön)

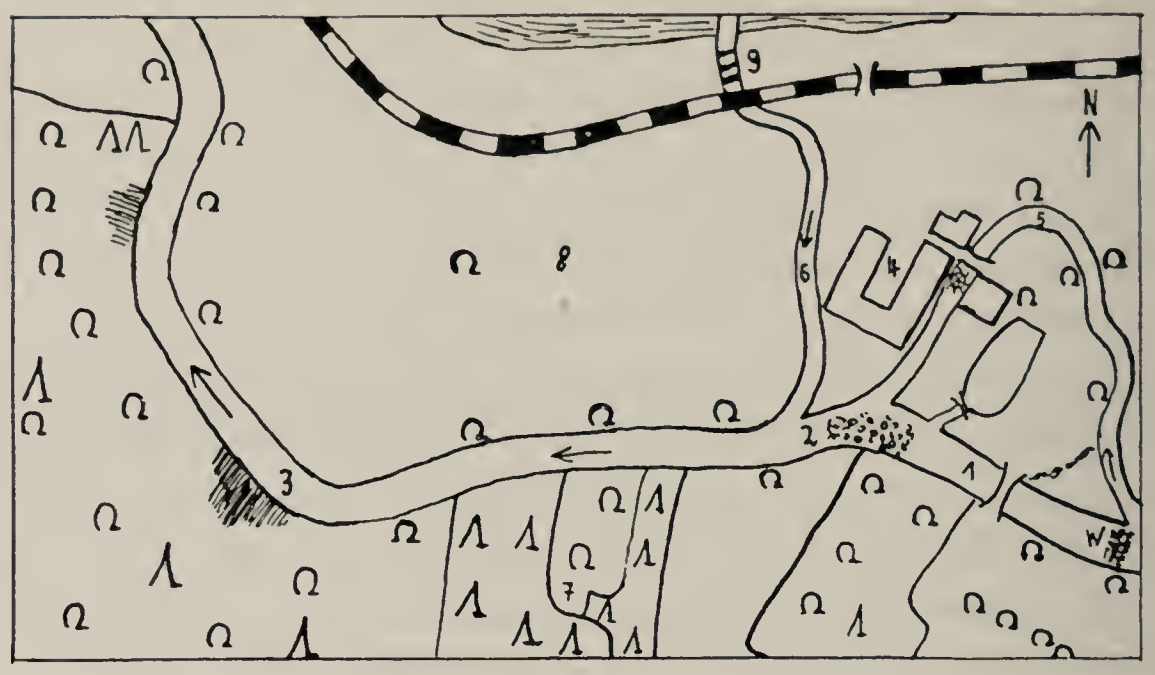
Das klassische Zeitalter der Vogelkunde begründeten heimatverbundene Männer wie die sachsen-anhaltischen Bauernornithologen NAUMANN, die Jahrzehnte und Generationen hindurch im engbergrenzten Gebiet der Heimat das Leben der Vögel, ihr Kommen, Verweilen und Wandern beobachteten, Vögel fingen, jagten, hegten, sammelten. Der thüringische Landpastor CHRISTIAN LUDWIG BREHM gehörte auch noch zur alten Schule; denn auch er vermochte noch durch selbstausgeübten Vogelfang jahraus jahrein im gleichen Gelände tiefere Einblicke zu gewinnen in das Vorkommen der Vögel und den Grad ihrer Ortsgebundenheit, als die meisten Feldornithologen späterer Zeit. Um Verbreitung, Standorttreue und Zug der Vögel zu erforschen, empfiehlt sich auch heute noch die Arbeit im engen Raum auf weite Sicht.

Der F a u n i s t wird selbst bei gesteigerter Aufmerksamkeit nicht den gesamten Bestand heimischer Vogelarten an einem Ort feststellen, wenn er nur kurz dort verweilt; schon Wetter und Lebensverhältnisse der Vögel können dies vereiteln, sind doch z. B. brütende Vögel oft für Wochen einfach unsichtbar, dazu halten sie sich stimmlich noch so zurück, dass sie selbst dem Fachmann unbemerkt bleiben. Feinheiten, wie die regelmässigen und abweichenden Lebensgewohnheiten, die zahlenmässige und jahreszeitlich wechselnde Häufigkeit, die Ab- und Zunahme, Verschwinden und Neueinwanderung der Arten werden nur dem Kenner offenbar, der lange in seinem Beobachtungsgebiet ausharrt und auch eine vollständige Liste der brütenden, durchziehenden und überwinternden Spezies zusammenzustellen vermag. Wir Faunisten wurden in den letzten Jahrzehnten mehrfach Zeugen mancher Wandlung, so des Häufigerwerdens oder Rückgangs der Arten, ihres Neuauftretens und der oft sprunghaften Ausweitung ihres Areals. Ich brauche nur zu erinnern an die Türkentaube, die Wacholderdrossel, den Tannenhäher. Schwer ist es oft, den genauen Zeitpunkt der ersten Brutniederlassung zu ermitteln, und deshalb sind, wie ich in Bezug auf die Wacholderdrossel sagte, »wichtig die ersten Brutnachweise an solchen Orten, wo der Vogel trotz sorgfältiger Beobachtertätigkeit tüchtiger Feldornithologen in früherer Zeit nicht bestätigt worden war» (Vogelring 1952). Ähnlich liegt es bei der Ansiedlung des Dickschnäbligen Tannenhähers in der hessischen

Rhön: in dem von mir schon mehrere Jahre oft und gründlich bearbeiteten Gebiet des Ulstertals begegnete ich dem Tannenhäher erstmalig am 27. 4. und 26. 6. 1941, wo ein Vogel bei Findlos-Batten zum Trinken an die Ulster kam und dann in demselben Wald verschwand, wo ich in späteren Jahren und heute noch die Art regelmässig antreffe. Wenn ich nicht zahllose Mal an der gleichen Stelle schon vorher gewesen wäre, so hätte meine Aprilbeobachtung von 1941 für die Frage nach der Einwanderungsgeschichte von *caryocatactes* nicht diesen Wert. Wenn Nachrichten über das »Fehlen» einer Art auch stets mit Vorsicht aufgenommen werden sollten, so wird man solchen Angaben umso eher Gewicht beilegen, je vertrauter mit der dortigen Ornis der Berichterstatter durch lange faunistische Arbeit eben in dieser Gegend erscheint. Neben die gewissermassen »negativen Befunde» mag man etwaige »positive» Beobachtungen aus Nachbarbezirken stellen und so den Arealwandel der Art aufhellen.

Vertrautheit mit der Gegend, ihrer Natur und Bevölkerung, Anwendung des Vogelfangs und der Beringung in einem begrenzten Raum mehren die Erfolge des Faunisten. Bei der quantitativen Ermittlung des Vogelbestandes können diese Voraussetzungen und Verfahren durch direkte Zählung (bei Beringung und Wiederfängen) die schönen Ergebnisse noch steigern, die besonders finnischen Forschern mit Hilfe anderer Methoden schon beschieden waren. Dann wird auch die mengenmässige Ermittlung der Vogelbesiedlung frei werden von den unsicheren Bezeichnungen wie »häufig», »selten» usw. und die Erkenntnis der vorhandenen Vogel-Massen mit manchem Vorurteil aufräumen und wichtige Grundlagen bieten für Forschung und Vogelhege.

Auf allen Gebieten der Ornithologie, welche die B e r i n g u n g als Forschungsmittel verwenden, wird nur eine langjährige Arbeit im gleichen Gebiet zufriedenstellende Resultate zeitigen. Hat man in den Anfangszeiten der Vogelberingung grossen Wert besonders auf Fernfunde gelegt, weil sie die Wanderwege und -ziele der Zugvögel zeigen, so sind die Orts- und Nahfunde erst in ihrer Bedeutung erkannt worden, als man in jüngster Zeit folgenden Fragen erhöhte Beachtung schenkte: Wie lange verweilt der Vogel am Brutort, dem Rastort, dem Überwinterungsort; bleibt er diesem treu, kehrt er dorthin (regelmässig?) zurück? Wie verhält er sich zu den Artgenossen, die mit ihm durch geschwisterliche oder eheliche Bande verbunden sind oder zusammen einen Schwarm bilden? Wann, wie und wo bilden sich die Gemeinschaften? Wir sind diesen Fragen seit Jahrzehnten durch unsere emsige heimatgebundene Arbeit nachgegangen, einiges davon wurde schon von meinem Mitarbeitern und mir in unserer »Vogelring»-Zeitschrift gebracht: Freitag (Vogelring 1936—1940) studierte die Eheverhältnisse beim Star, die Schlafgemeinschaften der Rauchschwalbe (1942), Mogall die Frage, wie die Meisen sich zeitlich und räumlich verhalten zu ihren Nist-, Futter- und Schlafplätzen (1935), ich zeigte an den Uferschwalben (1933) die regelmässige Rückkehr der Brutvögel zur alten Niststätte und bemühe mich jetzt um alle »Hessischen Ringvogelfunde» (Vogelring ab 1956), um für unser Land auch gerade die Nicht-Fernfunde für biologische Fragen



Erklärung zur Kartenskizze der Wasseramsel 7086074

W = Wehr
1 = Brücke
2 = Kiesbank
3 = Steinwand
4 = Hasenmühle
5 = Mühlgraben
6 = Laudenbach
7 = Waldtränke für Vögel
8 = Felder, Aecker
9 = Treppe m. Wasserfall

Brutplatz der Wasseramsel seit Jahrzehnten
Wa. 7086074 ♀ dort jung beringt Juli 1953
Brutvogel (1954?), 1955—1958 an Steinwand

Masstab: 1 cm = ca. 50 m

auszuwerten. Nach Abschluss der »Vögel Hessens» (1954) widmet sich meine Vogelkundliche Station Hasenmühle bei Tann/Rhön vorwiegend der Vogelforschung mittels Beringung im engen Raum auf weite Sicht und gewährt bei der jährlichen »Osterfreizeit» alten und jungen Vogelfreunden Einarbeitungsmöglichkeiten in unser Verfahren. Und da traf es sich 1958 wieder sehr günstig, dass starker Vogelzug Gelegenheit bot zu Vergleichen zwischen echten Zugvögeln und etwa den Zeisigen, deren Schwärme durch planmässige Beringung und Kontrollfänge auf ihr Verweilen, ihre Zusammensetung geprüft werden konnten (Bericht dorüber ist vorgesehen für die Zeitschrift »Luscinia» der Vogelschutzwarte Fechenheim). Andererseits setzte die Biographie der Wasseramsel 7086074 in Staunen, die seit 1953 hier ansässig, auch dieses Jahr wieder 5 Junge zeitigte (vergl. beiliegende Tabelle).

Hat mich schon früher bei dem »Standvogel» Wasseramsel die Beziehung des Nachwuchses zum Standort der Eltern und die Wahl des eignen Reviers beschäftigt

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Erklärungen

O = ber., beringt
dj. = diesjährig
nj = nestjung
♂ = Männchen
♀ = Weibchen
Wa = Wasseramsel

58/86 = 58 gramm/86 mm Flügellänge
( ) = Ringnummer nicht durch Fang nachgeprüft
(+) = Wa nicht gefangen, muss aber da sein
\+ = wiedergefangen

Wasseramsel ♀ Helgoland 7086074 als Beringungs-Beispiel »im engen Raum auf weite Sicht«

Jahr Tag	Fang-Plätze: Wehr	Brücke	Kiesbank	Steinwand	g/mm	Brut	Zusammen mit
1953							
25. 7.	beringt:			O			
23. 8.			+		58/86		
8. 9.		+			51/—		
24. 9.				+	51/—		
16. 12.		+			55/—		
1954[1]							
11. 3.				+	65/—		
24. 3.		( )				Wa baut unter	
2. 5.		+			63/—	Brücke (mehrere Nestanfänge in der Nähe)	
3. 7.	+						
17. 10.				+	51/—		
14. 11.		+			56/85		
1955							
(5. 4.)				( )		Nest mit 3 Eiern	
13. 4.				+	57.5/88		♂: 7051701 (ber. dj. 28. 6. 52 »Brücke«)
25. 4.				+		auf Nest 4 juv., 1	
4. 5.				(+)		Ei 4 juv. beringt	
12. 5.				( )		Nest leer	
24. 8.		+			55.5/—		
12. 10.			+		55/87		
1956							
22. 4.				+		auf Gelege i. vorjähr. Nest	♂: 7051701 (siehe oben!)
12. 5.				(+)		2 juv. beringt	
1957							
19. 4.				+		kleine juv.	
24. 4.				(+)		3 juv. beringt	♂: 8535198 (ber. dj. 19. 7. 56 Kiesbank)
(7. 6.)				( )		Kleine juv. II. Brut werden im Nest gefüttert	
(16. 6.)				( )		4 Nestlinge beringt	
1958							
12. 4.				+	60/85.5		♂: 7277313 (ber. dj. Steinwand 13. 8. 57)
1. 5.				+		auf neuem Nest	
(18. 5.)				(+)		5 Nestlinge beringt	

[1] 1954 konnte Nistplatz nicht sicher ermittelt werden.

(Vogelring 1940), so fand ich auch in den letzten Jahren immer wieder die Erfahrung bestätigt, dass die Jungen in ihren ersten Sommer/Herbst bald das elterliche Revier verlassen und schon im ihrem endgütigen Lebensraum heimisch werden. Die hier behandelte Wasseramsel ♀ 7086074 wurde als Jungvogel (unbekannter Herkunft) am 25. 7. 53 beringt genau an dem Prallufer aus Buntsandstein, wo er heimisch blieb (1955, 56, 57, 58 einwandfrei als Brüter nachgewiesen). Die männlichen Ehepartner waren 3 mal knapp einjährige Tiere. 1956 behielt unser Vogel Nest und Ehepartner von 1955 bei (Brutplatz seit Jahrzehnten immer von einem Wasseramselpaar besetzt).

Wenn ich hier mich auch der ständigen Hilfe junger Vogelfreunde und gelegentlichen Beistandes von Fachgenossen erfreue, so reichen doch Kraft und Zeit nicht aus, alle Vögel zu beringen und zu inventarisieren; dennoch wurde die auf die nächste Umgebung konzentrierte Arbeit belohnt durch eine gegen früher vervielfachte Zahl von Wiederfängen. Eine weitere Steigerung der Resultate ist zu erwarten, wenn unser Vogelring-Punkt, wie ich es schon 1932 vorschlug, ergänzt wird durch »gleichwertige Ketten von Vogelring-Punkten in der bevorzugten Zugrichtung unserer Zugvögel von Nordost nach Südwest» mit einer einheitlichen planmässigen Beobachtung, Beringung und Hege und sorgfältiger Ringvogelkontrolle.

Vergleichend-parasitologische Bemerkungen zur Klassifikation der *Procellariiformes*.

G. Timmermann

Hamburg

In meinem Vortrage vor dem »1. Internationalen Symposium für Wirtsspezifität und Parallelentwicklung bei Wirbeltierparasiten» im April vergangenen Jahres in Neuchâtel und einige Monate später in meinen »Studien zu einer vergleichenden Parasitologie der Charadriiformes oder Regenpfeifervögel» habe ich erstmals darauf hingewiesen, dass die vergleichend-parasitologischen Befunde die Annahme näherer verwandtschaftlicher Beziehungen zwischen den beiden Vogelordnungen der *Charadriiformes* und *Procellariiformes* nahelegten. Unter den Gesichtspunkten, die zur Entwicklung dieser Ansicht führten, stand unter anderem die Tatsache an entscheidender Stelle, dass die auf Regenpfeifervögeln weit verbreitete und für diese Ordnung typische Kopflausgattung *Saemundssonia* auch bei Sturmvögeln lebt. Da nun aber noch vor wenigen Jahren von urteilsfähiger parasitologischer Seite (Harrison 1937, Clay 1949, 1950) die Vermutung ausgesprochen worden war, dass die *Saemundssonia*-Vorkommen bei Sturmvögeln nur zufällige, durch ein gelegentliches Überlaufen von Fremdwirten zustande gekommene Einzelbefunde darstellten, denen eine Beweiskraft für stammesgeschichtliche Zusammenhänge nicht innewohne, erschien es erwünscht, diese Frage einmal an Hand des gesamten, zur Zeit verfügbaren Parasitenmaterials zu überprüfen, für dessen Überlassung ich in 1. Linie unserer verehrten Kollegin, Fräulein Dr. Clay vom Britischen Museum in London, zu Dank verpflichtet bin.

Zunächst einmal ergab das Studium der einschlägigen entomologischen Fachliteratur, dass *Saemundssonia*-Arten keineswegs ganz vereinzelt auf Sturmvögeln vorkommen, sondern bisher von nicht weniger als 12 Sturmvogelarten beschrieben worden sind, die sich auf 9 verschiedene Gattungen, nämlich *Macronectes, Fulmarus, Priocella, Puffinus, Pterodroma, Pagodroma, Oceanites, Hydrobates* und *Oceanodroma*, verteilen. Zu diesen konnte ich im Zuge der in Rede stehenden Untersuchungen 6 weitere neue *Saemundssonia*-Arten von 8 verschiedenen Wirtsvögeln aus den Gattungen *Daption, Pachyptila, Thalassoica, Pterodroma, Garrodia* und *Pelagodroma* beschreiben, nicht eingerechnet eine Reihe weiterer, augenscheinlich neuer Formen von *Puffinus*, für deren endgültige Charakterisierung mir zur Zeit noch ein aus-

reichendes Vergleichsmaterial fehlt. Selbst wenn wir annehmen wollen, dass sich einzelne der von Sturmvögeln berichteten *Saemundssonia*-Arten im Wege eines Typenvergleiches künftighin als identisch erweisen könnten, bleibt doch nach wie vor der bedeutsame Umstand als gesichert anzunehmen, dass wir zur Zeit von einem Viertel aller Sturmvogelarten typische, nur bei dieser Vogelordnung lebende *Saemundssonia*-Arten kennen. Bedenkt man hierbei, dass sich diese Anzahl nach den Erfahrungen mit anderen Gruppen ohne Zweifel bedeutend erhöhen wird, sobald man die *Procellariiformes* einmal systematisch, d. h. Gattung für Gattung und Art für Art, auf Kopfläuse untersucht, es zum anderen auch keineswegs ausgemacht, ja nach Lage der Dinge nicht einmal wahrscheinlich ist, dass *Saemundssonia*-Arten bei allen procellariiformen Abteilungen schmarotzen (ich denke hierbei besonders an die Albatrosse), wird man nicht umhin können, für die Arten der Gattung *Saemundssonia* eine weite und durchaus regelmässige Verbreitung bei Sturmvögeln anzunehmen, die schon als solche den Gedanken an eine zufällige Sekundärbesiedlung praktisch ausschliessen dürfte.

Es kommt hinzu, dass bereits eine oberflächliche Durchsicht der bei Sturmvögeln lebenden *Saemundssonia*-Arten ans Licht stellt, dass es sich bei diesen um durchaus eigenwillige, mit keiner der auf Möwen, Raubmöwen oder anderen Charadriiformes schmarotzenden Arten übereinkommende oder auch nur ähnliche Formen handelt, was Eichler 1949 veranlasste, die von Sturmvögeln kommenden *Saemundssonia*-Arten als *Puffinoecus* generisch abzutrennen. Wenn man sich diesem Schritt auch nicht anschliessen kann, weil die bei Sturmvögeln lebenden *Saemundssonia*-Arten ihrer Ausprägung nach keineswegs einheitlich sind, sondern eine Reihe recht unterschiedlicher Artengruppen bilden, unter denen »*Puffinoecus*» nur eine, nämlich die bei Wasserscherern (*Puffinus*) parasitierende, darstellt, so macht es die Summe der vom Standardtypus der Gattung abweichenden morphologischen Sonderheiten doch in hohem Masse wahrscheinlich, dass sich die *Saemundssonia*-Arten der *Procellariiformes* nicht erst heute oder in der jüngsten geologischen Vergangenheit auf den Sturmvögeln etabliert haben, sondern einen sich offenbar über lange Zeiträume hinweg ganz selbständig entwickelt habenden, ursprünglichen Besitz der Ordnung darstellen, den diese mit den verwandten *Charadriiformes* teilt.

Der Nachweis nun, dass die Verwandtschaftsverhältnisse der auf Sturmvögeln schmarotzenden *Saemundssonia*-Arten dem natürlichen System der Wirtsvögel folgen, würde die These, dass die *Saemundssonia*-Arten originale, d.h. stammesgeschichtlich gesprochen von Anbeginn an auf ihren Wirten lebende Sturmvogelparasiten sind, so gut begründen, wie dies mit den Mitteln der vergleichenden Parasitologie irgend möglich ist, d.h. praktisch unangreifbar machen. Die gedachte Beweisführung hängt jedoch im wesentlichen von der Erfüllung zweier Voraussetzungen ab, die vor der Hand nur in bescheidenem Masse gegeben ist, nämlich einmal von der Verfügung über eine leidlich vollständige Übersicht über die bei Sturmvögeln lebenden *Saemundssonia*-Formen und zum andern von der Möglichkeit, das parasitologische Bild mit einer phylogenetischen Klassifikation der *Procellariiformes* zu vergleichen,

die eine so verlässliche Nachzeichnung der natürlichen Zuordnungsverhältnisse innerhalb dieser Vogelordnung darbietet, dass sie als Richtmass dienen kann. Über die Lückenhaftigkeit unserer Kenntnisse, die *Saemundssonia*-Arten der Sturmvögel angehend, hatte ich schon gesprochen, und was das System der *Procellariiformes* anbetrifft, so hat mich das Studium der hier anknüpfenden Fragen und Probleme leider nicht davon überzeugen können, dass die Begrenzungen der einzelnen procellariiformen Gruppen und ihre Beziehungen zu einander in den derzeit gebräuchlichen Klassifikationen bereits einen wirklich adäquaten Ausdruck gefunden haben, was indessen nicht zu heissen braucht, dass diese Systeme deswegen ganz unbrauchbar wären oder hinsichtlich ihres Wahrheitsgehaltes wesentlich unter dem Niveau derjenigen anderer Vogelordnungen lägen. Ganz allgemein lässt sich wohl sagen, dass die Unsicherheit der verwandtschaftlichen Relationen mit der Höhe der systematischen Kategorien zunimmt; während die Zusammengehörigkeit der jeweils in eine Gattung geführten Arten in der Mehrzahl der Fälle ungefähr richtig erkannt sein dürfte (was bei der grossen Zahl monotypischer Genera freilich nicht weiter erstaunlich ist), scheinen hinsichtlich der Beziehungen der Gattungen untereinander und ihrer Zusammenfassung zu Unterfamilien und Familien noch recht erhebliche Unklarheiten und Meinungsverschiedenheiten zu herrschen. Das gilt insbesondere für den eigentlichen »Kern» der *Procellariiformes* mit den Familien der *Procellariidae* und *Hydrobatidae*, während die Eigenständigkeit der stärker sonderentwickelten Albatrosse und Tauchersturmvögel (*Pelecanoides*) nicht nur ornithologisch, sondern auch parasitologisch viel besser begründet ist. Soweit wir zur Zeit schon einen Überblick über die *Saemundssonia*-Formen der grösseren Sturmvogelgattungen besitzen, unter denen ich in erster Linie *Puffinus* und *Oceanodroma*, daneben aber auch *Pachyptila* (*Prion*) und *Oceanites* nennen möchte (aus der grossen Gattung *Pterodroma* kennen wir zur Zeit erst eine *Saemundssonia*-Art), findet sich der Sachverhalt der Parallelläufigkeit in den Systemen der Wirte und ihrer Schmarotzer auf eine überzeugende Weise erfüllt. So beherbergen 5 verschiedene *Puffinus*-Arten dieselbe Anzahl mehr oder minder deutlich unterschiedener *Saemundssonia*-Arten vom *Puffinoecus*-Typ, die sich in ihrer Verbreitung offenbar streng auf die genannte Wirtsgattung beschränkt halten; *Saemundssonia incisa* von *Oceanodroma leucorrhoa* schmarotzt auch auf *Oceanodroma tethys; Saemundssonia desolata* lebt sowohl bei *Pachyptila desolata* wie bei *Pachyptila forsteri* und auch *Oceanites oceanicus* und *O. gracilis* werden von identischen oder doch von einander sehr nahestehenden *Saemundssonia*-Formen parasitiert.

Sobald wir die durch den Umfang der Gattungen gegebenen Grenzen überschreiten und uns mit unseren Überlegungen sozusagen im intergenerischen Raum bewegen, wird das Auffinden als gesichert anzunehmender Beziehungen aus den dargelegten Gründen schwieriger. Immerhin beweist die parasitologisch durch gleiche oder sehr ähnliche *Saemundssonia*-Arten angezeigte Verwandtschaft der Hydrobatidengenera *Oceanites, Pelagodroma* und *Garrodia* einerseits und *Hydrobates* und *Oceanodroma* andererseits, dass sich der parasitologische Befund nicht nur in Überein-

stimmung mit der ornithologischen Gruppierung der Arten befindet, sondern auch die natürlichen Verwandtschaftsverhältnisse der Gattungen verlässlich nachzeichnet. — Der erste und bisher einzige Fall, der Anlass gegeben haben könnte, das in die vergleichend-parasitologische Methode gesetzte Vertrauen zu erschüttern, betrifft die verwandtschaftlichen Affinitäten unseres Eissturmvogels *Fulmarus glacialis*, der nach Massgabe seiner *Saemundssonia*-Art seinen nächsten und zwar allerengsten Verwandten (beide Vögel werden durch die gleiche Art parasitiert) in der antarktischen *Priocella antarctica* bzw. *glacialoides* besitzt. *Priocella* wird aber von PETERS in seiner »Check-List of Birds of the World» nicht nur generisch von *Fulmarus* getrennt, sondern sogar in eine andere Unterfamilie geführt. In dieser Frage hat sich jedoch mittlerweile der Fortgang der Forschung insofern gegen die bisherige ornithologische Systematik und für die parasitologische Aussage entschieden, als Herr Kollege VOOUS (Amsterdam) in einer neuerlichen Revision überzeugend dargelegt hat, und zwar wohlgemerkt ohne den Mallophagenbefund zu kennen, dass *Fulmarus glacialis* und *Priocella antarctica* kongenerisch sind und als geographische Vertreter einer und derselben Superspezies zu gelten haben.

Dass die erörterte, die Beziehungen zwischen Wirt und Schmarotzer steuernde Gesetzmässigkeit auch im Bereiche höherer taxonomischer Einheiten gilt, wird zum mindesten durch die schon erwähnte Tatsache angedeutet, dass *Saemundssonia*-Arten bei den beiden Familien der Albatrosse und Tauchersturmvögel bislang noch nicht gefunden worden sind und — was speziell die erste angeht — auch wohl kaum vorkommen dürften. Dieser negative Befund unterstreicht nachdrücklich die von ornithologischer Seite durch Gewährung von Familienrang geforderte Sonderstellung der beiden Gruppen und kann als weiteres Glied in einer Kette von Beweismitteln gelten, die samt und sonders dartun, dass die stammesgeschichtlichen Beziehungen der Kopfläuse bei den *Procellariiformes* weitgehend jenen Vorstellungen entsprechen, die wir in bezug auf die verwandtschaftlichen Verknüpfungen ihrer Wirte hegen. Damit wäre aber zugleich in hohem Masse wahrscheinlich gemacht, wenn ich hier einmal die Summe der bisherigen Ausführungen ziehen darf, dass die Mallophagengattung *Saemundssonia* nicht nur regelmässig und verbreitet auf Regenpfeifervögeln vorkommt, sondern auch einen echten Altbesitz der *Procellariiformes* darstellt und als solcher ein energisches Zusammenrücken dieser beiden grossen Vogelordnungen befürwortet.

Von weiteren, aus der Sicht der Gattung *Saemundssonia* angezeigten, aber vor der Hand ornithologisch noch nicht oder noch nicht ausreichend gesicherten Beziehungen möchte ich zunächst auf eine anscheinend nähere Verbindung zwischen *Fulmarus/Priocella* und *Macronectes* hinweisen, die bei aller Ungleichartigkeit im einzelnen eine natürliche Verwandtschaftsgruppe in weiterem Sinne bilden dürften. Sehr enge, durch den Besitz eines gemeinsamen Parasiten sich ausdrückende Relationen scheinen ferner zwischen den beiden hochantarktischen Gattungen *Thalassoica* und *Pagodroma* zu bestehen, denen sich *Daption* in einigem Abstande anschliesst. Von *Halobaena*, *Adamastor*, *Procellaria* und *Bulweria* sind zur Zeit noch keine *Sae-*

mundssonia-Arten bekannt geworden. *Puffinus* steht parasitologisch recht apart und könnte seine relativ nächsten Verwandten in *Pterodroma* besitzen, die nach Massgabe ihres *Saemundssonia*-Befundes die im ganzen einfacheren morphologischen Konfigurationen darbietet, doch muss hier das Ergebnis weiterer Untersuchungen abgewartet werden. Sehr bemerkenswert ist schliesslich der parasitologische Charakter der Gattung *Pachyptila*, die zwar einesteils deutliche Verbindungen nach der Seite der *Thalassoica*-Verwandtschaft hin zu erkennen gibt, anderenteils aber eine so starke, z.T. auch morphologisch gestützte Hinneigung zur *Oceanodroma*-Gruppe der *Hydrobatidae* bekundet, dass ihre Einbeziehung in die Familie der Sturmschwalben in weiterem Sinne kaum zu umgehen sein dürfte. Erleichtert würde dieser Schritt dadurch, dass auch die Sturmschwalben parasitologisch in zwei scharf geschiedene Abteilungen, die ihrer Zusammensetzung nach bereits flüchtig gekennzeichnete *Oceanites*-Gruppe und die *Oceanodroma*-Gruppe, zerfallen, von denen die letzte wiederum den Anschluss an Genera wie *Thalassoica, Pagodroma* und *Daption* sucht. Ob man soweit gehen sollte wie Garrod (1873) und nach ihm W. A. Forbes in seinem Bericht über die Sturmvögel der Challenger-Expedition (1882), die den kleinen Formenkomplex der *Oceanitidae* auf Grund anatomischer Erhebungen allen übrigen Sturmvögeln gegenüberstellen wollen, mag an dieser Stelle zunächst unerörtert bleiben. Tatsache ist jedenfalls, dass sich der durch die Mitte der Sturmschwalben hindurchgehende Schnitt auch parasitologisch sehr deutlich abzeichnet und es — ohne damit dem Ergebnis einer späteren, eingehenderen Überprüfung vorzugreifen — nicht nur vertretbar, sondern auch notwendig erscheinen lässt, *Oceanites* und *Oceanodroma* mit ihren Verwandten jeweils vorläufig in besondere Unterfamilien zu führen. Ein solcher Schritt würde wahrscheinlich zugleich den Anstoss zu einer dringend notwendigen Revision und Neuordnung nicht nur der *Hydrobatidae*, sondern auch aller, zur Zeit scheinbar ziemlich willkürlich in den Unterfamilien der *Fulmarinae* und *Puffininae* untergebrachten Gattungen geben, wobei die vergleichende Parasitologie dem ornithologischen Taxonomen in vielen Fällen bei der Aufhellung schwer durchschaubarer Verhältnisse und verborgener Zusammenhänge eine wertvolle, leider immer noch viel zu wenig in Anspruch genommene Hilfe werden kann.

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A Contribution to the Theory of Bird Navigation

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INTRODUCTION

The hypothesis that birds navigate by reference to the sun and other celestial bodies has received much attention in recent years. Extensive contributions to the subject have been made by several workers, notably G. V. T. Matthews and G. Kramer.

The principal weakness of the existing theories is the fact that a bird is supposed to be able to find the highest point on the sun's apparent diurnal path from a brief observation. In the opinion of the author this would make too great a demand upon the bird's sensory apparatus. It would be more satisfactory if it could be shown that it is possible for a bird to home successfully by reacting to the positions of celestial bodies only, without the necessity for perceiving their motions.

The author here attempts to show that successful navigation could follow from quite simple reactions to the position of the sun, provided that birds possess an adequate time sense or »internal chronometer». He does not, however, claim that this is actually the means by which birds navigate, as he has not had the opportunity for experimental work. This paper is intended merely to point out that the requirements for successful navigation are less than is usually supposed and to suggest a line of possible advancement towards a complete solution of the problem.

THE »INTERNAL CHRONOMETER»

An adequate time sense or »internal chronometer» is essential for successful solar navigation. Consequently, before considering the possible mechanism of navigation, it is as well to briefly recapitulate some of the evidence for the existence of such a »chronometer». Most investigations of time sense in animals appear to have been in connection with rhythmic behaviour in arthropods. An interesting example of these investigations is the work of Harker (1953), who showed that the 24 hour rhythm of ascent and descent in nymphs of *Ecdyonurus* is unchanged after five months in continuous light. A single exposure to the diurnal light cycle is all that is necessary

to establish the rhythm but nymphs which have no experience of illumination change show no rhythm.

In the case of birds there are the orientation experiments of KRAMER (1952) on Starlings *(Sturnus vulgaris)*. His results may be explained on the assumption that the birds possessed an »internal chronometer». HOFFMANN (1953) has shown that a trained orientation, with respect to the sun, is retained by Starlings after 23 days under constant light.

The evidence appears to favour the existance of an adequate time sense, which is probably based on metabolic changes of great regularity. The synchronization of this »internal chronometer» with the solar day seems to be accomplished by experience of the diurnal light cycle. Once such synchronization has been accomplished it apparently remains stable over long periods under constant conditions.

THE NATURE OF THE RESPONSE TO THE SUN

The response of a bird to the sun, when it is released in strange country, is, it is suggested, very simple. If the sun appears lower in the sky than it would at »home», at the same time, the bird flies in the general direction of the sun; if the sun appears higher, it flies away from the sun. In other words, the bird reacts to the sun much as it would to a tall landmark within sight of its »home»; if it were finding its way with the aid of the landmark.

A bird navigating in this manner follows a curve over the surface of the earth, which, after a while, will bring it to a point on the instantaneous position circle of its »home». (The position circle is a circle on the surface of the earth, for all points of which, the altitude of the sun is the same, at a given instant of time.) If the bird has not chanced upon a part of the circle near its »home», in a short while the rotation of the earth will change the position circle so that the bird is no longer upon it. The bird can then repeat the process described above until it again arrives on the »home» position circle. In general this process, repeated as necessary, brings the bird within striking distance of its »home» in a reasonable time.

It has, of course, been assumed that the bird has had a normal view of the sky in the period before its removal from »home».

THE PATH OF THE HOMING BIRD

The path of the homing bird consists of parts of complicated spiral curves, which may be constructed graphically on the map, by the method described in the Appendix. Figure 1 shows two example tracks. These tracks have been plotted for two imaginary birds homing from Cambridge to the Isle of Wight in May. It has been supposed that they both started at 10 00 hours and that perfectly windless and cloudless conditions prevailed throughout.

The faster bird, supposed to fly at 50 Km.hr^{-1}. arrives on its home position circle at 16 15 at a point only just over 50 Km. from home. It could probably home visually

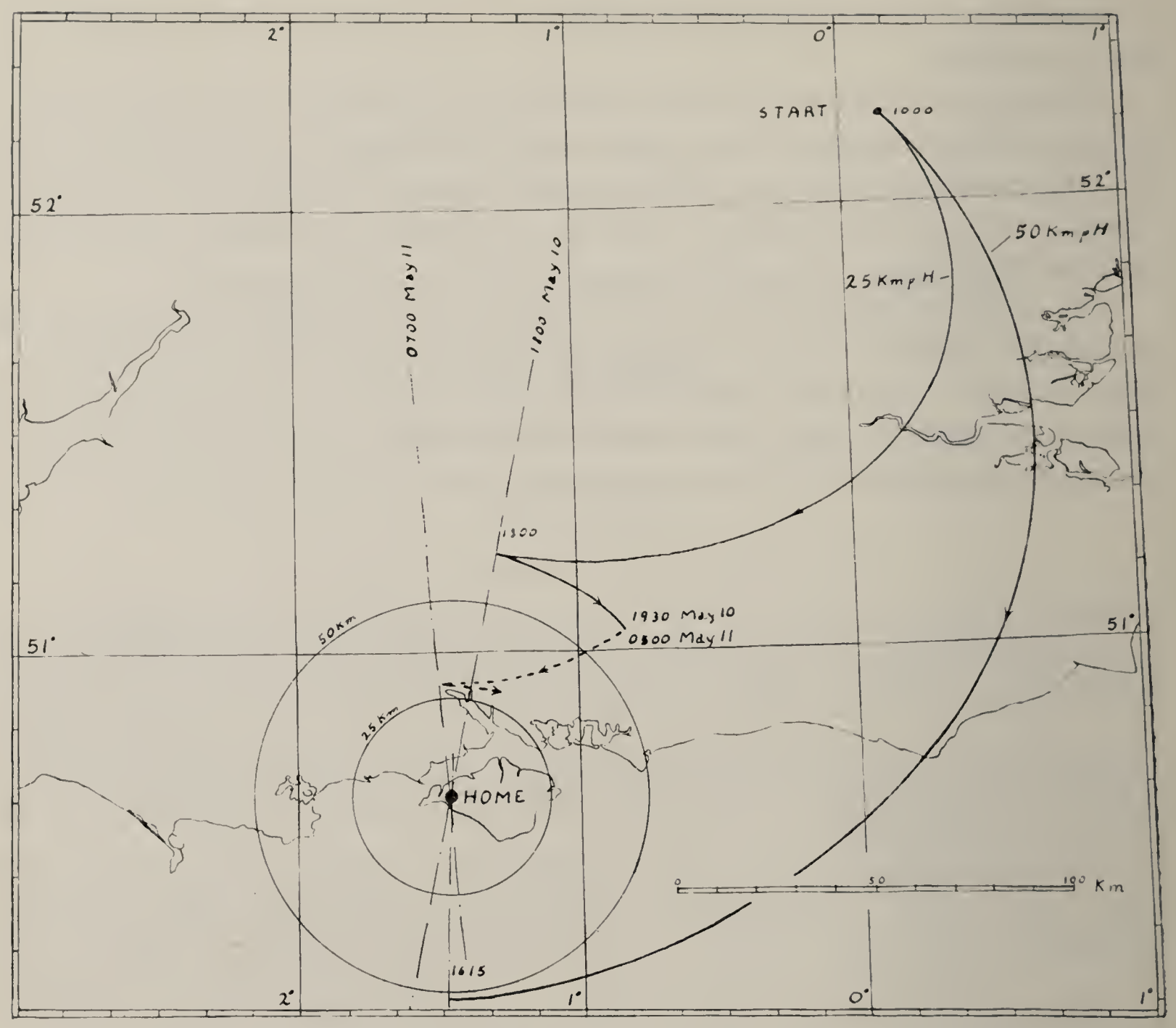

Fig. 1. Examples of the flight paths of homing birds.

from this distance, if not, it could continue to follow the position line as it rotates. To do so, however, it would have to reduce flight speed and would not approach much nearer before dusk.

The other bird flying at only 25 Km. hr^{-1}. does not reach the home position circle until 18 00, at a point north of home. In this case the circle passes the bird and it has to reverse its direction. It is overtaken by night at a point 60 Km. from home. The assumption is made that it proceeds no further at night and, the path that it would follow in the morning has been indicated. The home position circle is again reached at 07 00 near the mouth of the River Test and from here it should be able to home visually. Any effects of topography, *e. g.* meeting a coastline, have, of course, been neglected in these considerations.

For our next example we have a somewhat longer journey. The imaginary bird is supposed to have been released at a point on the Connemara coast in early July and to be homing to a place in South-Western Scotland. Furthermore it is supposed to sustain continuous flight at 30 Km. hr^{-1}. during daylight. Perfect conditions are

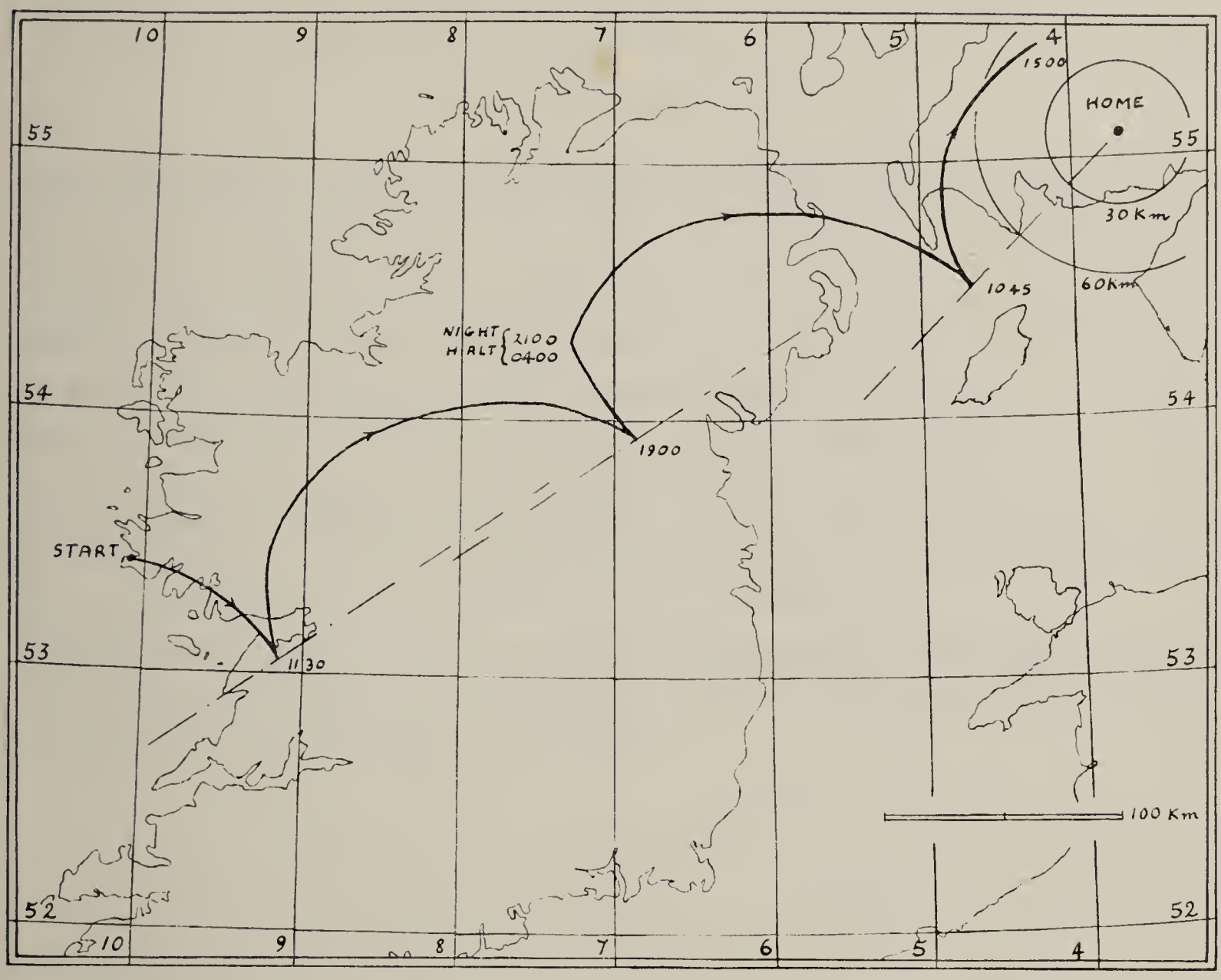

Fig. 2. Example showing a longer journey.

also assumed. The path in this case is more complicated, nevertheless at 15 00 the next day the bird has arrived at a point less than two hours flying time from home.

Lack of space prevents the author from giving the many examples required to give a thorough appreciation of the somewhat complicated paths by which birds would travel if they used this simple means of navigation. However, it is important to illustrate the effect of wind on the path. Figure 3 shows two tracks of birds flying between the same points as in figure 1 and, again, in May. In this case one track is for a bird flying at 40 Km. hr^{-1}. under windless conditions and the other shows what happens if a constant wind of 20 Km. hr^{-1}. blows in the direction indicated. The second track is quite seriously displaced, nevertheless, it still brings the bird within 60 Km. of home. It is quite possible that birds can recognize landmarks up to two hours direct flying time from home. While this one illustration must suffice it will indicate that although light winds are no great handicap, stronger winds of say, more than half the air speed of the bird are likely to disrupt the homing process entirely.

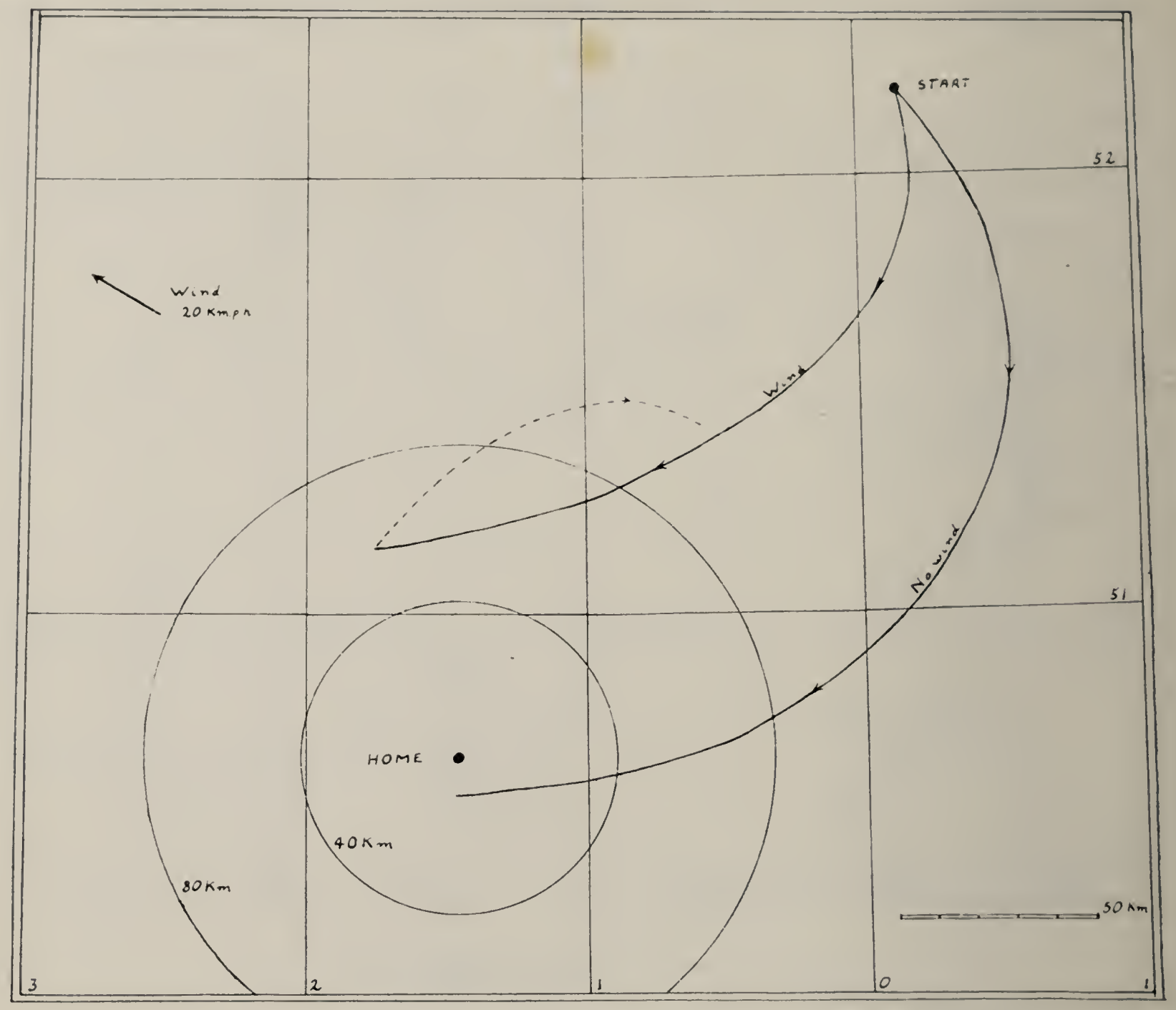

Fig. 3. The effect of wind on the flight path.

CONCLUSION

It has not been possible in the brief space available for the author to develop these ideas on bird navigation as fully as desirable. However, if this paper succeeds in demonstrating the possibility of successful homing by very simple responses to the sun's position it will have fulfilled its purpose.

It may be argued that the paths followed by birds using this method of navigation are excessively complicated. This argument has little weight, however, as although the tracks are complicated on the map, in fact they may be followed with comparitive ease. Great circle courses are not the simplest to follow and, at sea, human navigators have often used the apparently more complicated rhumb line course.

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APPENDIX

Construction of flight paths

The path may be constructed sufficiently accurately in hourly segments. The azimuth of the sun is found for a time half an hour after the start of the flight and a line in this direction is drawn through the starting point on the map. A segment equivalent to one hour's flying is marked off on the line, in the correct sense. The azimuth of the sun 1 $^1/_2$ hours after the start is next determined and the appropriate line laid down through the end of the segment marked off on the first line. Another hour segment is marked off on the new line and the process repeated as necessary. Care must be taken to change the direction of flight when the home position circle passes the bird. For small distances, *i. e.* up to about 500 Km. a straight line through home perpendicular to the sun's azimuth is a sufficient approximation to the position circle, as this is generally some thousands of kilometres in radius.

When obtaining the azimuth from tables, the approximate latitude and longitude of the bird at the time concerned should be used; this may be obtained with sufficient accuracy from the bird's last marked position.

The Proportions of Plumage, Organic Matter and Water Content in the Bodies of some Birds

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INTRODUCTION

The bird population of any ecosystem has three definite functions in its development: structure, dynamics and physiology. Besides this the bird population represents a part of the matter and energy circulating in the ecosystem and/or exchanged between the ecosystems. From the point of view of community ecology it is as important to know the materials and their proportions in the body of birds, as for other taxonomical, life-form or functional groups of organisms.

As there are some adaptive properties of birds to the ecosystems they inhabit, *e. g.* adaptations in structure, behaviour, food habits, breeding, activity etc., it can be supposed — by mere analogy to other animal groups and by causality — that there are in birds some adaptive properties, too, in the gross chemical composition of their bodies.

The present study has been carried out mainly in the interests of community ecology and — if possible — to draw some conclusions about the adaptive properties of the composition of the body in different birds.

MATERIALS AND METHODS

In the years 1956 to 1958 mainly forest birds were collected by shooting for stomach analyses. Some of these birds were analysed as to the ratio of plumage to body-weight, the water content and dry matter and the organic and inorganic matter in their bodies. Birds of 25 species were involved. Birds were collected mainly in Central and Southern Slovakia, but those shot outside the breeding season are of uncertain origin. Prior the analyses the birds were examined as to the race, status of moult and the general condition. The material examined is shown in Table 1.

Most of the birds are *Passeriformes:* they have been used mainly because of their relative small body size. Species of other orders were involved for a rough comparison.

The entire plumage of the birds involved was removed by plucking, then air-dried and weighed on an analytical balance to one milligram. The stomach contents were removed from the plucked body and it was then weighed to 0.1 gram. The ratio of plumage is expressed as *per cent* of the

TABLE 1

Bird species	Number examined		Total
	plumage	both plumage and body composition	
Galli:			
Tetrastes bonasia.....	1 ♀		1
Phasianus colchicus	1 ♂		1
Pici:			
Dendrocopos major	1 ♀	1	1
Passeres:			
Nucifraga caryocatactes ...	3 1 ♂ 2 ♀	1	3
Garrulus glandarius	2 2 ♂	1	2
Parus major	3 2 ♂ 1 ♀	2	3
Parus caeruleus.....	3 2 ♀ 1 ♂	3	3
Parus ater	2 1 ♂ 1 ♀	1	2
Parus cristatus	2 2 ♂	1	2
Parus palustris	4 2 ♂ 2 ♀	4	4
Aegithalos caudatus	2 2 ♀	1	2
Sitta europaea	4 1 ♂ 3 ♀	4	4
Certhia familiaris	2 1 ♂ 1 ♀	2	2
Certhia brachydactyla.....	1 1 ♀	1	1
Turdus merula	2 2 ♂	2	2
Sylvia curruca	1 1 ♀	1	1
Sylvia atricapilla	2 1 ♂ 1 ♀	2	2
Phylloscopus collybita.....	1 1 ♂	1	1
Phylloscopus sibilatrix ...	1 1 ♂	1	1
Regulus regulus	2 2 ♀	1	2
Lanius collurio	2 1 ♂ 1 ♀	2	2
Pyrrhula pyrrhula	3 2 ♂ 1 ♀	3	3
Fringilla coelebs	3 1 ♂ 2 ♀	2	3
Emberiza citrinella	2 1 ♂ 1 ♀	2	2
Passer montanus	1 1 ♂	1	1
Total:	51	40	51

body weight. Of the 49 passerine birds examined as to the ratio of plumage, 18 birds were in moult, while 30 were outside the ekdysis. So were the three birds of other orders. From the particular percentages of species of *Passeres* the arithmetical mean percentage, the standard deviation and standard error have been calculated. Besides this, the mean percentage for each passerine family was calculated to find out whether this deviated from the grand mean.

The body of birds without stomach content (but with stomach dissected) was placed into an electric dessicator at 100—110° C until a constant weight was obtained. The difference between the original weight and the weight after drying was considered to be the water content of the body and expressed as a percentage of the original body weight (without plumage). The remainder is the dry matter.

The dry body was then analysed as to its organic and inorganic matter by placing it on a platina-dish followed by combustion according to STOLTE's method. The ash was obtained usually after one hour's combustion. The difference between the weight of the body before and after com-

bustion is considered to represent the organic matter. This is expressed as a percentage of the dry body weight. In four birds (Table 2) the inorganic matter, or ash, was further analysed by lye-washing in 20 % HCl. The particular minerals are expressed as per mille of the dry matter of body weight.

TABLE 2

Bird species	Amount of minerals, per mille of the total dry matter						
	SiO_2	Fe_2O_3	CaO	MgO	SO	P_2O	KCl and NaCl
Parus caeruleus ♀	0.5	1.3	6	1.2	2	48	73
Parus ater ♂	0.7	0.7	7	1.6	2	50	58
Sitta europaea ♂	0.8	7.6	8.8	5	3.4	47	48
Sylvia curruca ♀.....	0.7	9.3	1.5	5	4.6	42	68

Acknowledgements are due to Mrs. VIKISÁLY for laboratory assistance and to Mr. POHL-REICH, assistant chemist, for chemical analyses.

RESULTS

a. Ratio of plumage

The ratio of plumage to the total body weight was calculated *post mortem, i. e.* the body with plumage, but without stomach contents. The contents were removed to eliminate their influence on the weight of the bird bodies.

In passerine birds the mean relative weight of the plumage was 9 %, with a range from 5 to 12 %, s (standard deviation) 1.8 and s_M (standard error of the mean) 0.26, coefficient of variation $V = 20$. In gallinaceous birds the mean percentage is 8.5, while in *Pici* it is 7 %. The mean relative weight of plumage *(per cent)* in the particular families of *Passeres* is, as follows:

Family	mean	range	Family	mean	range
Corvidae	8	7— 9	Sylviidae	8	6—11
Paridae	10	9—12	Regulidae	11	10—12
Sittidae	8	5— 9	Laniidae	7	7— 7
Certhiidae	10	11—12	Fringillidae	9	7—12
Turdidae	7	6— 9	Passeridae	7	—

It may be supposed that in the specimens in moult the ratio of plumage is not comparable with those not in moult. In fact, if the percentage of plumage weight is calculated separately for the birds in moult and outside moult, we find it to be 8.3 % and 9.4 %, respectively. Thus the birds in moult have on an average less plumage than others do. The difference is however, not significant in a »t-test», values for P between 10 and 5 per cent being obtained.

No conclusions could be reached from the material examined about any differences in the ratio of plumage according to age, sex or season.

b. Water content

Because the material was exposed to a variable loss of moisture during transportation, loss of blood, duration of plucking etc., the water content is the most variable property examined. Therefore the dry matter is too. In passerine birds the mean water content, $M = 67$ %, with $s = 2.7$, $s_M = 0.43$ and $V = 4$, where $n = 39$. The range is 58 to 72 %. The mean value is close enough to that found in mammals, *e. g.* 65 %. In one woodpecker (Table 1) the water content was also 67 %.

The mean water content *(per cent)* of the body of birds in particular families is, as follows:

Family	mean	range	Family	mean	range
Corvidae	69	68—71	Sylviidae	64	58—69
Paridae	67	64—69	Regulidae	65	—
Sittidae	69	66—70	Laniidae	66	65—67
Certhiidae	66	66—67	Fringillidae	69	68—70
Turdidae	71	71—72	Passeres	69	—

From these results it follows that the body of birds consists only of 33 per cent dry matter, out of the original dead weight without plumage and stomach contents.

c. Organic matter

In a total of 39 passerine birds the mean of the percentage of organic matter, out of the dry matter, has been found to be $M = 88$ % with $s = 1.5$, $s_M = 0.24$, $V = 2$, range from 82 to 91 *per cent*, where $n = 39$. In one woodpecker the organic matter made 88 %. According to the families the percentages are, as follows:

Family	mean of the organic matter	mean of the inorganic matter	range of organic matter	Family	mean of the organic matter	mean of the inorganic matter	range of organic matter
Corvidae	83	17	82—84	Sylviidae	89	11	88—91
Paridae	87	13	86—88	Regulidae	88	12	—
Sittidae	86	14	85—86	Laniidae	88	12	88—89
Certhiidae	87	13	87—89	Fringillidae	87	13	86—88
Turdidae	88	12	87—88	Passeridae	87	13	—

On average the bodies of birds examined contained 12 *per cent* ash. The ash of four birds has been additionally analysed by lye-washing in 20 per cent HCl. The participation of the particular minerals is shown in Table 2, as the per mille of weight of the dry matter of the body. Although the analysis shows differences, striking in some mineral substances, the material is indicative and orientative only.

DISCUSSION

The results here presented are of a preliminary character for the materials involved are unsatisfactory for general conclusions. The analyses made, indeed, indicate a relative homogeneity of the birds examined in the composition of their bodies. This fact is of great importance in community ecology.

Plumage on average accounts for 9 *per cent* of the total body weight and this percentage is the most constant amongst the properties examined. The range from minimum to maximum percentage is 7 *per cent* only. So far as the materials examined allow, it can be stated that smaller birds have relatively more plumage than larger birds, which is due to their relatively greater body surface with correspondingly greater heat loss per unit weight. It is of interest to show that the warblers *(Sylviidae)* are the most variable not only in the amount of plumage, but in the water content, organic and inorganic matter in their bodies. This needs more study, based on the taxonomy, evolution and ecology of this group of birds. The relative constancy of the amount of plumage, however, does not exclude the possibility of some taxonomically usable racial differences within species and superspecies respectively.

The water content of bird bodies accounts on average for 67 *per cent* of the body weight and, with a range of 14 per cent, is the most variable property examined. Thus, whatever may be the possible error due to the methods used, the birds accumulate a large amount of water in their bodies and in this they are closely related to mammals. The great variability in water content indicates also some adaptations to habitat and food.

The ratio of organic matter in birds is rather high, accounting for 88 *per cent* of the dry matter of body. Again, this property proved to be relatively constant, for the range is only 9 *per cent* The inorganic matter was also relatively constant in proportion. The amount of organic matter is of special interest in community ecology, for it reflects in some way the production of organic matter in the community (ecosystem). In this connection I will draw attention to the problem of biomass. This is defined — as well as used — as the weight of any group, sum or population of organisms. The purpose of calculating the biomass and using it in community ecology is to calculate and characterize the production within the ecosystem. As the inorganic matter (water, minerals) is not produced, except the metabolic water in the ecosystem, but only circulates and is accumulated and dispersed, the true biomass is the organic matter only, stored and accumulated in the bodies of the animals, respectively produced and stored in the plants. Therefore what we use in community ecology as biomass, *e. g.* the weight of organisms, contains but a part what could be called the true biomass. This is the organic matter. I have calculated this true biomass as the percentage contributed by the organic matter to the total body weight of birds *post mortem*, thus including the plumage and excluding the stomach contents. In the 39 passerine birds the mean is: $M = 26\ \%$, $s = 2.3$, $s_M = 0.39$ ans $V = 9$. The range is from 23 to 34 *per cent*, *i. e.* 11 *per cent*. This mean value is the true biomass of the passerine birds. It should be corrected for the organic matter of the plumage, in particular the epidermal proteins, which were not dealt with in these analyses. Roughly it can be said that in the birds examined the biomass is 26 per cent of the total body weight. Only the biomass so expressed indicates the partial production within the ecosystem, the value of birds in the food-chains and the amount of potential energy accumulated by birds.

Unfortunately, the paucity of the materials examined does not enable us to draw any conclusions about the adaptive characters of the properties examined. Therefore the present preliminary report fulfils only the one synecological purpose, mentioned in the introduction of the present paper.

Summary

1. In 51 specimens of 22 species of *Passeres*, one species of *Pici* and two species of *Galli* the ratio of plumage has been examined and expressed as the percentage of the total body weight *(post mortem)* without the stomach contents. The mean values are in *Passeres* 9 %, *Pici* 7 % and *Galli* 8.5 %. The results indicate a negative correlation between the amount of plumage and body size.

2. In 40 specimens of 22 species of *Passeres* and one species of *Pici* the water content of the body of birds was examined by dessication. Birds examined contain on average 67 *per cent* water or, in turn, 33 *per cent* dry matter.

3. The same birds, as sub. 2., have been analysed for the content of organic and inorganic matter in their bodies, dry matter, respectively. The birds examined had 88 *per cent* organic and 12 *per cent* inorganic matter, out of the dry matter of their body.

4. The author suggests the use of the amount of organic matter in the bodies of birds (and other organisms) to express the true biomass, instead of the biomass hitherto used, *e. g.* the total weight of birds (or other organisms) in any ecostystem or part of it. It was found that the true biomass, or organic matter is on average 26 *per cent* of the total weight of birds.

Some Aspects on the Directing and Releasing Influence of Wind Conditions on Visible Bird Migration[1]

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A survey of recent literature on bird migration reveals a lack of unanimity in the opinions of different authors concerning the factors releasing bird migration and the general effects of wind conditions upon visible bird migration. Disregarding the profound factors of a physiological nature, such as metabolic changes etc., several meteorological factors have been assumed to play more or less important roles for bird migration and its release, as will appear after even a brief review of modern literature. For lack of space, this review cannot be carried through on this occasion.

However, the data upon which the different hypotheses are based have been collected under widely different circumstances. First, there may be a rather sharp limit between diurnal and nocturnal migration. Second, the geographical positions of the bird stations from where most of the underlying material comes are widely different, and so is the topography of their environments. The result obtained is of course also deeply affected by the specific composition of the migrating birds. In this communication, the discussion refers to diurnally migrating birds, such as pigeons, birds of prey, and certain passerines.

A purpose of this paper is to call attention to the importance of the geographical position of the observation locality and of the wind conditions for the results obtained in studies on bird migration. This will be attempted through considering a model situation, *i. e.* an imaginary, schematic geographical area without minor topographical features, with all the coasts cut sharp, and without islands in sight from the coast-line. Far away, off the west coast of the land-mass, we shall, however, introduce a small oceanic island. We shall consider the bird migration at three separate localities, *viz.* A) on the small oceanic island, B) at the south-west corner of the la nd-mass, and C) at an arbitrary locality in the central part of the area.

The birds migrating through this area are to be regarded as completely uniform: we shall imagine all to possess a south-westerly primary direction = standard direction (*cf.* GEYR VON SCHWEPPENBURG 1949), *i. e.* when not influenced by any topo-

[1] Report from the Falsterbo bird Station No. 6.

graphical or atmospherical or other similar factors, they will keep a south-westerly course. They are further assumed to be affected by the only guiding-lines existing, *i. e.* the coasts.

Which external factors need be considered to be of importance for the course of the migrating birds over the area? First, there are the coasts. The flight-paths will converge towards the south-west corner because of the guiding-line effect, as may be exemplified from investigations in many parts of the world. Second, wind conditions will deeply influence the flight-lines. No variable factor has, according to my opinion, so far been discovered to be comparable to wind in importance for the course of migrating birds, and I shall hence restrict myself to a consideration of this factor.

It is true that birds tend to counteract the influence of wind upon their flight-paths. This reaction reduces somewhat the deviating effects of wind, but assuredly it does not render wind conditions insignificant for the course of migrating birds (see *e. g.* RUDEBECK 1950).

Let us now consider the passage of the migrating birds over our schematic area under a selection of different wind conditions. The facts on which the following discussion is based have only partly been published, in several different contexts. The sources cannot possibly be reviewed in this brief communication. I would like, however, to draw the attention to three investigations of great interest in this connection, *viz.* the account of the behaviour of the birds of prey on passage over south-west Scania (Skåne, SW. Sweden) by RUDEBECK (1950), the researches of Dutch ornithologists on the migration of the Chaffinch *(Fringilla coelebs)* over the Netherlands (DEELDER 1949), and some recently published observations on the course of migrating birds over the Danish Islands (BRUUN & SCHELDE 1957). The relevant facts are schematically represented in Fig. 1.

1. In *calm weather* only topography will affect the flight-lines over the area. The theoretical uniform distribution will be disturbed only by the guiding-lines of the coasts. Hence, there will be a concentration of migrating birds in the south-west corner. The absolute figures will be much higher at B than at A and C. Since in calm weather migration will generally proceed at some altitude, numbers are to be expected to be only moderately high at B, for as is well known, birds flying high are less influenced by guiding-lines than are low-flying birds.

2. With *head-wind* of moderate strength migration will attain maximal intensity at B, and the same would apply also to C under the assumption that head-wind has a directly stimulating effect on the release of bird migration. Guiding-line efficiency will be very strong, because the birds fly rather low. At A, consequently, there will be very few birds. With rising wind velocities migration will be still stronger at B in comparison to A and C, but the absolute figures will gradually decrease. This is because strong winds gradually inhibit the migration, whilst guiding-line efficiency will be still stronger. With falling wind velocities conditions will gradually approach those prevailing in calm weather.

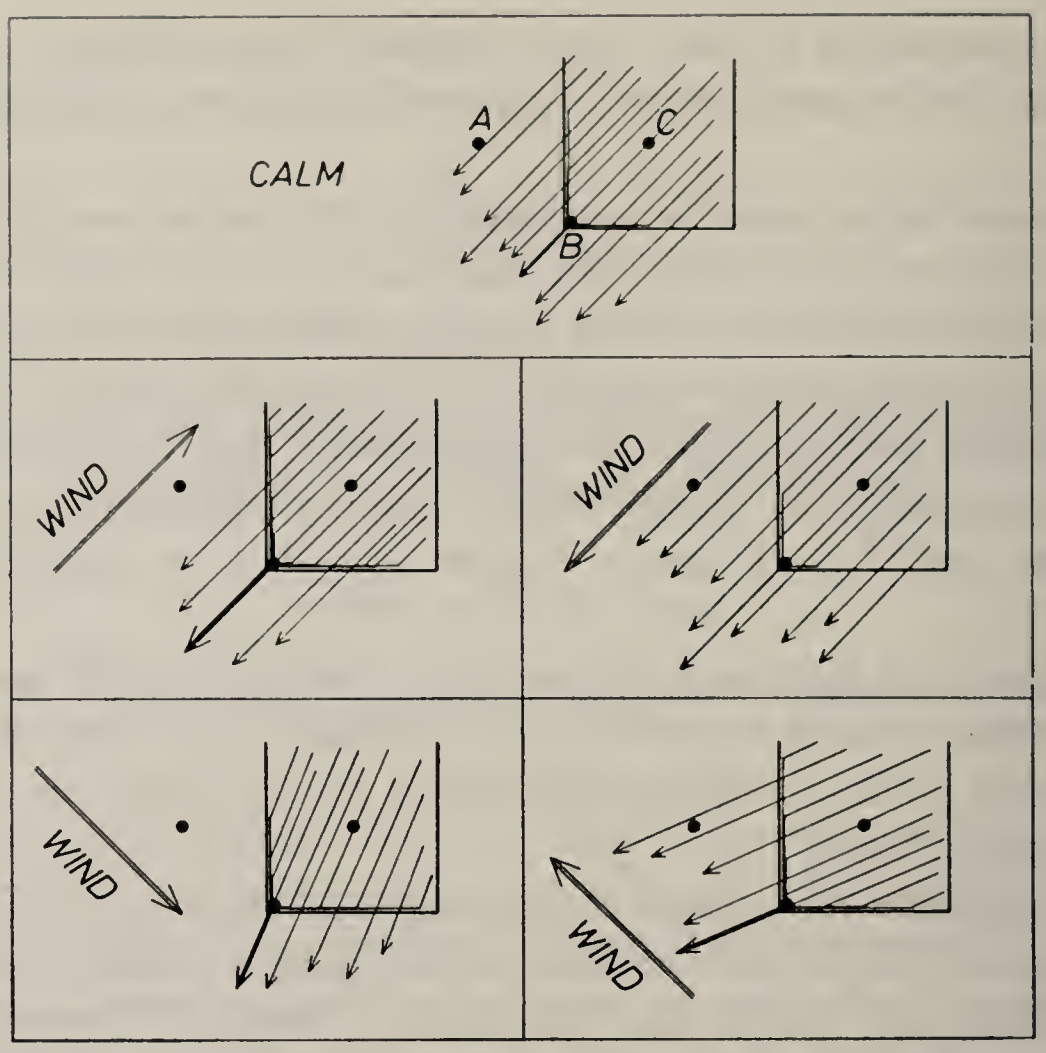

Fig. 1. Schematic representation of the course of bird migration over the imaginary land-mass. See text.

3. With *tail-wind*, conditions change fundamentally. Guiding-line efficiency will be low because of the rising average height of the migrating birds. The birds will thus pass out over the sea on a more »broad-front» migration. Comparatively low figures will be recorded at B, and also at C figures will be lower than with head-wind. A, on the other hand, will get relatively high figures. With rising wind strength migration intensity drops more or less quickly, whilst with falling wind velocities, conditions of course gradually approach those prevailing in calm weather. It should be borne in mind, though, that it is under these circumstances that birds are most likely to be overlooked. It is very difficult indeed to assess the importance of this source of error.

4. Let us now consider a situation with winds coming in from the *north-west*, *i. e.* at an angle of 90° in relation to the primary direction inherent in the birds. The paths of the migrants will be affected by this wind, hence the migration is deviated. Additional to this effect is the circumstance that the birds will strike the coast-lines at new angles, a fact of great importance for their reactions. The combined effect will be that there will be very few if any birds at A and moderate numbers at B and C. Strong winds will of course have greater effect, whilst very light winds will cause little disturbance.

5. Side-winds from the opposite direction, *i. e.* the *south-east*, will in principle cause similar effects. A sharp difference in the resulting distribution of the migrating

birds is, however, that relatively many birds are to be expected on the island observatory. From the view-point of an observer on this island, this may be described as a kind of drift migration (*cf.* WILLIAMSON 1955 and other works).

Let me take but one example, partly from RUDEBECK's (1950) work at Falsterbo, partly from a previous study by the present author (ULFSTRAND 1958). In years with predominant south-easterly to easterly winds during the migration period of the Honey-buzzard *(Pernis apivorus)* this species obtains relatively low annual totals at the bird observatory at Falsterbo (Scania, Sweden), but in autumns with persistent westerly to north-westerly winds the annual figures are much higher. It was shown by RUDEBECK *(op. cit.)* that this is because in the former case the birds are drifted off their path and pass over Zealand (Sjaelland, Denmark) to the west of Öresund instead. It appears that southerly and south-easterly winds have a much stronger deviating effect than northerly and north-easterly winds. This can probably be explained through the different topographical properties of the Scanian coasts. The west coast is indented by many bays and there are a number of capes protruding towards the west and south-west. Also the migrating birds will normally be able to see the opposite coast before leaving Swedish land. The south coast, on the other hand, is cut sharp and there are neither bays nor promontories, and finally the distance to the coast on the far side of the water surface is much greater. The opposite land is most often out of sight for the migrating birds when they are passing over the Scanian coast-line.

Let us summarize the above discussion and see how migration intensity will vary at the three observatories during a series of days with different wind conditions. The suggestions made above are plotted in Table 1, in which migration intensity is represented by a scale ranging from zero to five.

TABLE 1

Relative intensity of visible migration at the three observatories A, B and C during different wind conditions. The absolute figures are very different for A, B and C.

	calm	head-wind			tail-wind		NW	SE
		l.	m.	s.	m.	s.	m.	m.
A (island)	xxxx	xx	x	0	xxxx	xxx	0	xxxxx
B (corner)	xx	xxx	xxxxx	xxx	xx	x	xx	xx
C (central)	xx	xxxx	xxxxx	xx	xxx	xx	xx	xx

l. = light wind
m. = moderate wind
s. = strong wind

It is apparent from the table — which is, after all, but a summary of the foregoing discussion — that the pictures obtained at the three different localities are not in complete agreement with each other. Considerable discrepancies exist. Workers at the three stations would arrive at widely divergent conclusions about the relationship between wind conditions and bird migration and about the meteorological

factors releasing bird migration. The insight obtained through the above discussion is that it is very difficult, even impossible to make general decisions on many problems of bird migration from studies at one place only. This is especially true if studies are being carried out at localities situated on prominent guiding-lines or on an isolated island where the birds will appear only under special circumstances. One has constantly to keep in mind this dual aspect of bird migration: what caused the birds to start their migration flight, and what made them pass this or that way? It would appear that the best localities for investigations of these problems are inland places with the most uniform environments possible.

Now, is the imaginary area and its bird migration as described above relevant for real conditions? I believe that that is the case. We may transfer the simplified picture outlined above to several European districts. The model was constructed chiefly on the basis of experiences in the south part of Sweden, which has, however, no observatory »A», a very notable observatory »B» (*i. e.* Falsterbo), and where I have carried out field investigations on a locality corresponding to »C». No doubt, however, our picture may be transferred to the North Sea area with Helgoland as »A» and probably some Danish and German capes showing »B» conditions. Indeed, I think that the whole of western Europe may in a general way correspond to the schematic area outlined above with certain islands to the west of the European continent representing »A». Some promontories on the sea-border will exhibit conditions comparable to our locality »B».

Assuredly, the combined effects of topographical and meteorological factors involve a complex problem. I think that some advance in our concepts may perhaps be gained by considering model situations where different factors are analysed apart from each other. The discussion has demonstrated that the geographical and topographical characteristics of the observation spot and its environment exert a considerable influence on the picture of the process of bird migration obtained.

Several studies have been carried out concerning the influence of wind conditions on bird migration: its course, and how this is affected by the wind. This is far from saying that this aspect has been exhausted. On the contrary, much remains to be done. Now, what might be said in this connection concerning the influence of wind on the release of migration? First, I would like to emphasize once again that generally no broad conclusions on meteorological stimuli releasing bird migration should be drawn from investigations performed at only one locality. This is because of the fact that the bird »avalanches» (Svärdson 1953) as recorded at a bird station of traditional site are but a selection of all the avalanches in the given region. Some will remain unnoticed or be strongly underestimated because of the effects of the wind on the bird stream. For instance, it would appear justifiable to assume a positive effect of head-winds on the migration release in birds of prey at Falsterbo, but such a conclusion is unwarranted (Ulfstrand 1958). I would not say that head-winds do *not* exert such an influence, only that the material collected at this place alone does not permit definite conclusions. It might be that head-winds merely contri-

bute to the concentration of flight-lines and that they are of no great significance in releasing migration. However, investigations in other localities have demonstrated with some probability that head-winds under some circumstances do have a directly stimulating effect on migration and that is why, in the discussion presented above, I have supposed migration intensity to be maximal with head-winds. A more definite solution of the problem may be obtained from studies at suitable localities, where the concentrating effects of wind are of less importance than they are at, for instance, Falsterbo. Some of the assumptions made by different authors that there is a positive correlation between head-winds and migration release seem to have been unwarranted, for very often the field work was performed where migration is likely to be especially intense with head-winds, but this for purely topographical reasons.

Parenthetically, it should be pointed out that the conclusions arrived at in the above discussion would not be invalidated if it is proved that there is no such correlation between head-winds and migration release.

It is very probable that many factors have contributary effects as stimuli releasing bird migration. Wind may well be one of them. I believe that some advance in our views on bird migration might be gained through an ethological approach to the various problems. It is, I think, quite in agreement with modern ethological considerations that such a complex behaviour pattern as bird migration should be controlled by several releasing mechanisms and that it should be released only under rather special external (and internal) circumstances. If only one factor were to be responsible for the release of migration, the chances for a successful conclusion to migrational adventures would surely be reduced. Only when a certain accumulation of factors all with positive effects is at hand, migration starts. Some of these releasing stimuli are well known: temperature, visibility, thermal air-currents, physiological status and many other factors. All of them cooperate, but sometimes one factor is the chief one, sometimes another. Many other factors are to be assumed to be of importance, such as wind conditions and the presence of species companions in gregarious species. One may turn the problem upside down and direct one's attention in the first place to the factors inhibiting bird migration, an aspect suggested by NISBET (1957). Birds with badly balanced releasing mechanisms will be at a strong selective disadvantage, whilst well adjusted individuals will have much greater chances of survival. To be well adjusted to migrational performances is a matter of life or death for migratory birds.

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Sur l'ecologie de *Gyps fulvus* en Espagne

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Nous avons fait figurer sur la carte toutes les colonies connues de *Gyps fulvus*, en tout quelque 140, qui cependant ne représentent probablement que les deux tiers de la population existant actuellement. On constate aussitôt que le nombre de Vautours fauves existant en Espagne est très élévé. Il dépasse probablement 5,000, mais nous ne croyons pas qu'il atteigne 8,000 individus. La plupart des colonies se trouvent dans les zones basses des montagnes voisines des grandes plaines, qu'elles soient des vallées — bas Guadalquivir, Ebre — ou des plateaux — les deux Castilles. Il faut avouer que nous ne connaissons pas les colonies des Pyrénées ni de la zone montagneuse au N.W. du Guadalquivir.

Le nombre de colonies est d'autant plus élévé que la région est montagneuse, sans pourtant que la densité de population de Vautours fauves soit beaucoup plus forte dans les montagnes. Nous voulons seulement dire que dans les montagnes les colonies, de moindre importance, sont plus éparpillées. En plaine, où les rochers propices à la nidification sont rares, on trouve des colonies pouvant compter une centaine de couples. En montagne on trouve des couples relativement isolés.

On peut noter également l'absence des vautours dans le Levante, zone trop aride. On pourrait constater aussi que dans le nord, où le nombre de colonies est élevé, le nombre d'individus est faible, cette zone étant trop humide.

L'ALIMENTATION DES VAUTOURS FAUVES

Les vautours se nourrissent du bétail mort. C'est donc le bétail qui conditione leur distribution et leur abondance. Les proies les plus fréquentes sont:

Les Equidés. — Il y en a environ deux millions et demi, distribués partout, mais rares dans le Levante aride. Les mulets sont, avec les brevis, le bétail réellement abondant dans les plaines. A leur mort, les cadavres des mulets sont traditionellement laissés dans les champs pour les vautors et les chiens.

Les Vaches. — Il y en a environ trois millions et demi. Elles ne sont abondantes que dans les régions humides; zone cantabrique, zone occidentale, montagnes du centre, bassin inférieur du Guadalquivir. Elles sont toujours destinées à la coucherie; donc il est bien évident que leurs cadavres ne se trouvent pas dans la nature que rarement.

Les Brebis et les Chèvres. — Il y en a environ 20 millions de têtes, dont quatre millions de chèvres. Elles sont abondantes partout en plaine là où la vache ne peut pas vivre. Elles sont rares dans les plaines du S.E., et souvent, elles sont transhumantes, passant l'hiver en plaine et l'été en montagne. Elles sont destinées au boucher, mais chaque année des milliers meurent dans les champs.

Il faut présenter maintenant quelques considérations sur l'influence du bétail dans la distribution des vautours.

I. — Bien que le nombre de vautours ne soit pas connu avec précision, on peut estimer que pour chaque vautour il y a environ 5,000 têtes de bétail. Peut être — cela est très hasardeux — y-a-t-il environ quinze cents à deux mille équidés qui meurent chaque année, dont beaucoup sont dévorés par les vautours.

II. — La distribution des colonies de vautours dans la zone limitrophe entre les plaines et les montagnes, permet aux oiseaux de profiter de deux types d'alimentation différents, les equidés des plaines et les brebis, les chèvres et les vaches des montagnes.

a — Les Equidés, les mulets surtout, qui constituent le bétail de labour des plaines, des steppes à céréales, trop pauvres pour la pâture des vaches — sont conduites mourants à des places déterminés près des villages et laissés là sans être ensevelis. Cela fournit aux vautours une source de nourriture

assez régulière qui profite probablement surtout aux jeunes, très grégaires, et qui doivent vivre plutôt en plaine les premiers années de leur vie.

b — Les brebis et les chèvres, quelque peu aussi les vaches et les chevaux, qui meurent en montagne par accident ou de maladie et qui ne peuvent pas être récupérés par les bergers. Ce bétail joue peut-être le rôle le plus important dans l'alimentation de quelques unes des colonies de vautours.

On sait qu'une grande partie de ce bétail est transhumante. Les vautours se font aussi transhumants. Dans les hautes Pyrénées, les vautours apparaissent dans les premiers jours de mai pour disparaitre après la fin de septembre. Il semble que les colonies d'hiver de la Navarre soient désertées pendant le même temps. La même chose se passerait dans la Sierra de Guadarrama. A Arcos, dans le bas Guadalquivir, les oiseaux désertent la colonie d'hivernage à la fin de février pour se diriger vers le groupe de colonies signalé sur la carte, d'où ils ne reviendront que vers la mi-septembre.

III. — Dans le nord, aux paturages riches, le bétail le plus abondant est constitué par les vaches, laitières ou de labour. Les cadavres ne sont pas abandonnés dans les champs et les vautours n'ont rien à manger dans les vallées. En montagne ils ne trouvent que les victimes des accidents et des loups. Il en résulte une faible densité de vautours, qui sont probablement aussi transhumants en grande partie.

IV. — Dans le S.E. et l'Est, régions extrémement arides, il n'existe presque pas de bétail de labour ni de bétail laitier, du fait par les chèvres et les brebis, groupées en petits troupeaux bien gardés. Le vautour n'y trouverait jamais une proie et, en fait, il n'en existe pas.

De l'emsemble de ces faits nous pouvons déduire comment est conditionnée la distribution des vautours fauves dans la zone paléarctique occidentale. Pas d'aliments dans l'Europe humide où prospèrent les vaches, donc disparition des vautours au delà des Pyrénées, ne se maintenant qu'en montagne dans le sud de la France. Pas d'alimentation non plus dans les zones trop arides du pourtour méditerranéen, d'où forte diminution des vautours au Maroc Oriental, en Algerie et en Tunisie. On ne retrouvera peut-être des conditions semblables à celles de l'Espagne que dans les Balkans.

LA PLACE DU VAUTOUR FAUVE DANS LA BIOCÉNOSE NÉCROPHAGE

Un animal mort, abandonné dans un champ, peut être la proie, en Espagne, de predateurs variés. Il est à distinguer parmi ces prédateurs une phase diurne et une phase nocturne, mais nous n'avons pas à parler ici de la seconde, constitué principalement par des mammifères. Seul nous considérerons les animaux diurnes, parmi lasquels les vautours occupent une bonne place.

a) *Pica pica.* — La Pie.

b) *Corvus corone.* — La Corneille noire.

c) *Corvus corax.* — Le Grand Corbeau.

Les premières espèces à arriver auprès d'un cadavre sont les corvidés. Ces trois espèces sont en général incapables de rompre la peau de l'animal et elles se contentent de picorer les parties molles, langue, yeux, blessures, caillots de sang. Leur rôle, très important, est de signaler l'appat aux oiseaux de plus grande taille.

d) *Milvus milvus*. — Le Milan royal.

e) *Milvus migrans*. — Le Milan noire.

f) *Neophron percnopterus*. — Le Percnoptère.

Après les corvidés commencent à apparaitre les petits rapaces. Ils essaient de rompre la peau. Le percnoptère extrait les yeux, vide l'intestin quelquefois, mais le cadavre reste pratiquement intact malgré leurs efforts.

g) *Aquila chrysaëtos*. — L'Aigle royal.

h) *Aegypius monachus*. — Le Vautour moine.

i) *Gyps fulvus*. — Le Vautour fauve.

L'Aigle royal ne se présente que très irrégulièrement et seulement quand il n'y a pas de vautours. Le Vautour fauve et le Vautour moine sont les prédateurs principaux. Les *Gyps*, plus batailleurs et plus nombreux que les *Aegypius*, tentent plus ou moins d'éliminer ceux-ci. Les percnoptères, qui sont restés dans la voisinage, attendent les débris perdus. Les grands vautours mangent tout, à l'exception de la peau, trop forte dans les animaux fraichement morts, des os et aussi, quelquefois, l'intestin gonflé de paille.

j) *Gypaetus barbatus*. — Le Gypaète.

Il semble que le Gypaète attende la fin du repas des vautours. Il mange les os, que le plus souvent il avale sur place, ou que plus rarement il emporte pour les rompre sur les rochers. Il digère entierement la matière osseuse et ne régurgite que les sabots des brebis et des chèvres.

Les chiens jouent un rôle important dans la biocénose diurne. Très souvent, ils arrivent avant les vautours. En plaine, les mulets laissés à coté des villages atirent toute la population canine du lieu. Les chiens rompent facilement la peau — souvent au bénéfice des vautours, qui profitent de l'occasion pour attaquer le cadavre — et en mangent la presque totalité. Les chiens craignent les vautours et leur abandonnent la place quand ces derniers deviennent nombreux.

En réalité, donc, il n'y a compétititon qu'entre les vautours fauves, les vautours moines et les chiens. Les vautours fauves dépendent à un certain degré des corvidés et des petits rapaces qui leur signalent la présence des proies. Il n'y a pas compétition avec les Gypaètes, qui mangent ce que les vautours ont laissé.

On peut supposer que dans le passé les vautours dépendaient largement des loups, des ours et des lynx pour l'apport des proies, sans doute principalement constitués par les cerfs, les sangliers et les chevreuils. Mais tous ces animaux aiment plus ou moins les lieux à végétation dense, les bois. Or, le vautour des bois c'est *Aegypius monachus*, plutôt que les *Gyps fulvus*. La déforestation, le remplacement de la faune primitive par le bétail actuel, le dénichage des oiseaux, très facile pour *Aegypius* qui niche dans les arbres, ont dû provoquer la diminution de ces derniers en faveur des *Gyps*.

What are *Ciconiiformes?*

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The earliest systems of classification of birds were based principally upon one or more external characters such as the shape of the bill, the wing and tail formula, foot and plumage structure, and less often upon characteristics of habit. The fallacy of attempting to found broad conclusions upon such a narrow basis was apparent to many ornithologists. Subsequently new systems were worked out by anatomists who based their classification upon the structure and relative positions of the palatal bones, or upon pterylography, or upon the arrangement of the carotid arteries, or the number and arrangement of the intestinal loops, or upon the pattern of the pelvic and leg muscles, etc.

Consequently the assessment of the taxonomic and phylogenetic status of birds was based on the comparison of individual characters in isolation, and not on the total anatomic pattern or taxonomic potentiality. These early classifications were very valuable guides to a better understanding of evolution but, in fact, they were nothing but intricate catalogues dealing with the modifications of one or another anatomical or morphological feature.

In the past only a few ornithologists have realised that there is no universal guiding criterion for classifying birds and that a lot of morphological and anatomical data must be collected in order that the system should be judged by the totality of the factors and characters involved in the course of phylogenetic differentiation.

From that viewpoint Huxley, Forbes, Parker, Garrod, Gadow, Fürbringer, Beddard, Mitchell, Shufeldt, Pycraft, Lowe and others did much to bring together a great amount of anatomical data and factual information for the arrangement of the higher taxonomic categories and recent outlines of avian classification have grown out of just such a multitude of studies on anatomic pattern. In his very valuable system Wetmore has generally emphasized dissimilarities more than resemblances and evaluated morphological and anatomical characters to generic, family or ordinal status. On the contrary in their outline of classification Mayr and Amadon laid greater weight on morphological resemblances than on anatomical dissimilarities in order to simplify systematics and to bring avian classification

more into harmony with that of other less well known groups of animals. Their handsome procedure is undoubtedly very interesting to museum workers on bird skins, but to focus too much attention upon structural resemblances or to minimize anatomical differences recalls to mind an old fashioned procedure which claimed that taxonomy is an art, not a science as we believe, and consequently nothing but a matter of personal opinion or judgment.

As long as there is not yet a procedure of universal applicability all classifications based upon reliable morphological, anatomical, ethological, parasitological, and physiological data are, in my opinion, successive approximations to the final system. But I disagree with those based upon the principle of simplifying systematics and consequently undervaluing evolution on mere philosophical or practical speculations.

It is a fundamental principle of taxonomy that a closeness of resemblance in total morphological potentiality is an indication of a corresponding closeness in zoological relationship. Consequently not only should resemblances be taken into consideration, but also an amount of anatomical, ethological and other information about dissimilarities and evolutionary trends; because a character may seem to be phylogenetically stable and reliable in one group and not in another, just as an evolutionary trend may be a most valuable indication for kinship in a genus or tribe but not in a family. Anatomists know that morphological variation is the rule, not the exception, although there is a basic typical design for each avian genus, family or order.

Therefore no new outline of classification should be worked out without broad anatomical justification and in order to eliminate the subjective factor as far as possible it is quite essential to decide general taxonomic relationships by reference to morphological resemblances so far as those may be determined by direct comparison of all the components of the total anatomic potentiality.

We do not yet need new philosophical approaches, nor new interpretative methods for a better understanding of speciation, distribution and adaptive phenomena in birds as long as we do not have complete information about bird's anatomy. By the way we especially need osteological data because in my experience, the myological, nervous and vascular systems are less stable than the components of the skeleton of adult birds.

There is evidence that functional stress may shape the bone, that a change of strength or direction of forces could lead to changes in the form and structure of bones and that modifications in the muscle function, related to a change in habit, generally are reflected in the skeleton. However it is true that changes in habit are subordinated to gene mutations which progressively give rise to evolutionary trends and consequently to differentiation and speciation.

On reviewing the order of *Ciconiiformes*, which embraces the *Ardeae*, *Balaenicipites*, *Ciconiae* and *Phoenicopteri*, no less than 174 taxonomical characters have been studied comparatively. Most of these characters are reliable data about pterylographical, anatomical and osteological features, and no character has been considered

as particularly important, nor as without any significance. Resemblances and dissimilarities figure side by side and a multitude of evolutionary trends were used in grouping related species.

The study will be published in full in the bulletin of the Belgian Royal Institute of Natural History and as it is very long I can not give any more than the outline of the new classification of the *Ciconiiformes* based upon the anatomical study of 24 species, upon the osteological comparison of 62 species and upon the literature bearing upon the subject.

The *Phoenicopteri* should be dropped out. They are distantly related to the *Anhimiformes* and to the *Plataleinae*.

Balaeniceps and *Scopus* are good representatives of suborders, owing to the large number of their peculiar characters.

The *Ardeae* and the *Ciconiae* are not intimately related; they are also good suborders.

The *Ardeae* include a single family of highly specialized birds with three tribes, of which *Cochlearius, Ardea* and *Botaurus* are the typical genera.

The *Ciconiae* are heterogeneous. I recognize two families; the *Ciconiidae* and the *Plegadidae*. In the former we have four tribes with *Mycteria, Anastomus, Ciconia* and *Leptoptilos* as typical genera. The *Plegadidae* are composed of two distinct subfamilies: the *Plegadinae* and the *Plataleinae*.

The *Ciconiiformes*, as a whole, are related on one side to the *Phoenicopteriformes* through the intermediary of the *Plataleinae*, at the other side to the *Charadriiformes* through the *Plegadinae* and finally to the *Pelecaniformes* through *Balaeniceps*.

The Problem of Flocking in Birds

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A flock of birds is a very ordinary occurrence, so ordinary in fact that it is only recently that ornithologists have turned their attention to this aspect of bird behaviour. The more spectacular numbers associated with migration have certainly aroused interest, but the emphasis has been on the migration and not on the aggregation of the birds into a flock. This coming together of birds has been referred to in a number of ways: it has been called a flocking tendency, a gregariousness, or a sociability, and attempts have been made to define the general phenomenon or isolated particularised manifestations of it. The most recent statement on these lines which also summarises the views of previous workers is by EMLEN. For the purpose of this paper the terms flocking and gregariousness will be used.

It is obvious that there is a great range in the degree of gregariousness shown by different species of birds which is very largely correlated with their way of life. There are species which are always solitary, various birds of prey, eagles, large raptors, etc. Then there are the large number of species which form loose flocks at one time of year or another, usually at migration times, other species stay in flocks during the winter, *e. g.* various passerines. Again there are the species which are much more closely integrated into flocks during the winter, *e. g.* the waders, and so on through all gradations to those species which are gregarious all the year round, including the breeding season, *e. g.* rooks, gulls, etc. This variation on a widespread theme suggests that the phenomenon of flock formation evolved quite early in the history of birds, in response to situations where it would be an advantage. This aggregation of numbers for mutual benefit is a very well known and much discussed zoological phenomenon, so that situations in which the members of a group have an advantage over the solitary individual will come easily to mind. The most obvious of these which might have selection value in the case of birds is against predators, for the awareness of a group is equal to the awareness of its most alert member and the probability of a predator being seen is increased in proportion to the size of the group. Another such factor might be the availability of food, aggregations occuring where there is food present, for where there is food for one individual there may be food for others. Also

group feeding is more efficient for food disturbed by one member and lost to it, as for example in the case of insects disturbed from grass, will very probably be eaten by a neighbouring individual. It is obviously possible to continue citing similar instances of the advantages of the group over the individual at considerable length and it is not difficult to provide justification for the early evolution of gregarious tendencies in birds. The fact that this gregarious tendency resulting in the formation of flocks is now so varied in its manifestations in different species suggests that it has itself undergone evolution along with those species, and that subsequent evolution has been towards the development of aggressiveness between individuals. These are difficult hypotheses to prove, but observations on the flocking behaviour of particular species may provide some answer to the general problem.

Looking at a flock we see a collection of birds. They may be calling to one another; they may be silent; they may be feeding, resting or even roosting. The questions which present themselves are: How close is the bond between the individuals? What is its nature, and how is it maintained? In the North of England in the rather isolated region of the Yorkshire Pennines is an area which annually serves as a gathering ground for migrating Curlew *(Numenius a. arquata)*, where these birds pause for a period of two to three months on their migration into Ireland to undergo their post-breeding moult. There is a strong indication that the first arrivals join the local breeding population which thus forms the nucleus of a flock which grows to a maximum of about 3,000 in early August. Watching the formation of this early flock in late June or early July the picture is of a small group of birds on the ground and a group of perhaps 5 or 6 flying in overhead. There is a continual exchange of calls between these two groups of birds, and the flying party appears to search visually for the area from which the answering calls are given, and when they have located it they circle and then drop down to join the birds on the ground. Later in the season there is no exchange of calls in this way and the airborne birds seem to join the flock by relying on visual stimuli only. In the case of Curlews therefore the exchange of call notes between birds coming in to join the flock and those already on the ground as a flock gradually diminishes as the duration of the flock in the area increases. This means that the bond between individuals changes from an initially loose one to a much stronger one as the daily routine of the flock becomes established. Another point which illustrates this is the behaviour of individual birds within the flock. In the early flock the birds are often in widely differing states of activity, some sleeping, some merely with their heads down, others with necks up, yet others actively walking about, but as the flock becomes established the percentage of birds in a similar state of activity is much higher, with much less diversity throughout the flock. The flock as a whole is also much more settled and less prone to unnecessary alarm, *e. g.* aeroplanes. It is interesting in this connection to note that workers on loosely integrated flocks find that there is a continual interchange of call notes, *e. g.* as found by HINDE in Tit flocks, whilst in the more highly integrated wader flocks this is replaced by a much softer conversational note when the flock is active. This flock gradually

establishes a daily rhythm in which the whole flock spends the day using the area as a day roost. Towards evening the flock begins to break up into smaller units which go off to feed, and it is then that these smaller units use the call notes to maintain contact with each other throughout the night. This highly integrated flock is thus consolidated into a small roosting area by day and is spread out into a loosely integrated flock covering several square kilometers at night.

During the day when the flock has been settled for some time, practically all the birds are asleep and there is a range of response to any disturbing conditions that is not seen in a more active flock. If a disturbance arouses such a flock the sequence of response is first awareness, then alarm, and finally flight, but at any one moment there will be birds at all these stages. They do not therefore rise as one flock, whilst certain birds will be well in flight as a small flock, followed by a series of stragglers, other birds remain on the ground showing alarm, some with their necks up and calling, others just with necks up, and a small residue still asleep. Indeed it sometimes happens that such a sleeping residue is in fact left behind when the rest of the flock moves elsewhere. When such birds finally wake up they immediately utter calls of the contact-making type and make circling flights before flying off, as if in search of the rest of the flock. This behaviour on waking is induced by the absence of the rest of the flock, for it has been seen several times when no outside disturbance affected the birds. This type of behaviour can only be explained on the assumption of a flock conciousness, that is, that there is a basic gregariousness in birds which causes them to show signs of distress when it is not satisfied, and initiates a form of appetitive behaviour. Several workers have noted this distress when birds are separated from their companions — MOYNIHAN and HALL, in the case of the Spice Finch *(Lonchura punctulata)* and LACK in the Long-tailed Tits *(Aegithalus caudatus)*.

It has been generally accepted that many species of similar type to the Curlew are gregarious outside the breeding season but lose this capacity when showing their characteristic territorial behaviour during the breeding season, or at least that this tendency is supressed by the aggressiveness consequent on attainment of a physiological state associated with breeding. One of the functions of territory is therefore to space out the breeding birds in the suitable habitats, but in the case of the Curlew this does not replace the social instinct for it appears to be necessary for the various pairs in an area to be in vocal contact and the breeding displays usually involve most of the birds in the immediate vicinity. It is very noticeable in this area where most of the observations have been made that the birds in any given breeding grounds all tend to produce their eggs about the same time, those in the valley head being about two weeks earlier than those on the higher ground. This is much more the characteristic associated with social breeding birds of the type described by FRASER DARLING. It seems therefore that in the Curlew the gregarious tendency is not ever lost even in the breeding season and it is suggested that the function of territory in this species is that it represents the pair distance for the species. This is comparable to the individual distance first postulated by CONDER, but whereas the individual

distance is relatively small, about 4 inches EMLEN found for Cliff Swallows *(Petrochelidon pyrrhonota)*, and CONDER for Starlings *(Sturnus vulgaris)*, and about a foot for Curlew in the post-breeding flocks, the pair distance would need to be much greater to allow the various stages of pair formation and breeding to take place uninterruptedly. The aggressiveness associated with the onset of the breeding season therefore serves to establish the pair distance by the same means that a bird keeps its own individual distance in a flock, but on a much larger scale and involving both members of the pair. The Curlew is then an entirely social bird in which gregariousness is always present, the bird keeping its individual distance in the flock and the pair keeping their pair distance in the breeding grounds by means of their territory.

It is interesting to consider how far it is possible to regard this as a more generally applicable concept. A survey of the literature on pair formation and territory demarcation has not yet yielded any serious misfits. In this connection the passerines seem to conform quite well to the hypothesis that there is a basic gregariousness in birds evolved fairly early in the history of the group and showing itself now in winter flocks where birds keep their individual distance and in summer breeding areas where the pairs keep their pair distance by means of their territories. The birds which have been regarded as the social types, rooks, gulls, geese, are probably those which have retained the more primitive gregariousness in which the pair distance is not much greater than the individual distance, whilst the more highly evolved types from this point of view are those which appear most independent. The birds of prey form an interesting illustration. The species which is colonial, the Lesser Kestrel *(Falco naumanni)* is the insectivorous form; other members of the group require a hunting territory and are therefore solitary species. Here is a group in which most members have evolved a way of life incompatible with the basic gregariousness which remains to become apparent only at migration times. The game birds in which the cock has no part in the nesting, or care of young, cycles, are difficult to fit into the general pattern unless these stages are regarded as belonging to the breeding cycle for which the pair distance is necessary, but the male is not. Having reached these conclusions it is gratifying to find that KOSKIMIES working with Blackgame *(Lyrurus tetrix)* and Capercaillie *(Tetrao urogallus)* reaches very similar conclusions. In fact from general discussion amongst ornithologists it becomes very apparent that any serious worker is driven to the conclusion that there is a basic gregariousness in birds, for to cite only the commonest factor quoted, there may be acres of suitable habitat but in any given area the birds of a particular species, and sometimes also of differing species, are to be found in fairly close proximity. The first worker to draw attention to this fact appears to be KULLENBERG.

It certainly seems therefore, that we can regard gregariousness as a basic characteristic of birds which evolved early in the history of the group, and that birds have undergone adaptive radiation away from this basic gregariousness by the increase of aggressiveness between individuals in response to differing modes of life.

The various phases in the life history, depending on different physiological states, and creating differing spatial demands, will have served to channelise the various behaviour patterns for each species.

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The work of the British Bird Observatories

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The British bird observatory network is unique, and its recent growth constitutes one of the most important developments in the science of ornithology. Only two observatories were operating before the war; but since 1945 hardly a year has passed without the establishment of one or more new stations, until today 15 are officially recognised by the Bird Observatories Committee which looks after their joint interests, and acts as a liaison body with the Council of the British Trust for Ornithology. The observatories are autonomous, but all have agreed to a standard system of record-keeping, the microfilm copying and central collation for study purposes of their records, and the co-ordination of different branches of their work through a Migration Research Officer recently appointed by the Council of the B.T.O. under a 5-years grant received from the Nuffield Foundation.

These widely scattered stations are mostly on small islands and headlands around the North Sea, English Channel and Irish Sea coasts; they are listed, with the date of foundation, in Table 1. There are in addition several embryo bird observatories working on similar lines which may develop in the near future (as others before them have done) and receive official recognition.

Bird observatory work has an important educational element, since the officially recognised stations provide accommodation and study facilities for students and amateur bird-watchers, and encourage such visitors to take an active part in the field and laboratory work devised by the warden or the governing committee. Their financial resources are slender, and most depend upon public subscription; and as only half are able to employ a warden it is difficult to ensure continuity of research, or promote special long-term studies. It can be said that the great progress which migration study has made in the British Isles during the past decade has been due in a large measure to the enthusiastic support of a large body of amateur workers.

FIELD-WORK

At all stations the chief occupation is the day-to-day recording of the numbers of birds and kinds of species present in a restricted area; from these records, short-term changes in the migratory populations can be deduced, and regional comparisons

TABLE 1

British Bird Observatories

Date Founded	Location	How organised
1934	ISLE OF MAY, Firth of Forth, Scotland.	Midlothian Ornithological Club.
1936	SKOKHOLM, Pembrokeshire, S. Wales.	West Wales Field Society and Field Studies Council.
1945	SPURN POINT, Kilnsea, E. Yorks.	Yorkshire Naturalists' Union.
1947	LUNDY, North Devon.	Lundy Field Society.
	NEW GROUNDS, Slimbridge, Glos.	Wildfowl Trust.
1948	FAIR ISLE, Shetland.	Fair Isle Bird Observatory Trust.
1949	GIBRALTAR POINT, Lincolnshire.	Lincolnshire Naturalists' Trust.
	CLEY and BLAKENEY, Norfolk.	Local committee.
1951	MONKS' HOUSE, Seahouses, Northumberland.	Private (Dr. E. A. R. Ennion)
	JERSEY, Channel Islands.	Societe Jersaise.
	GREAT SALTEE IS., Co. Wexford, Eire.	Local Committee.
1952	DUNGENESS, Kent.	Committee of Kent Ornitholog. Soc., London Nat. Hist. Soc., and Hastings Nat. Hist. Soc.
1953	BARDSEY, Lleyn Pen., Caern., N. Wales.	Friends of Bardsey Observatory.
1955	PORTLAND BILL, Dorset.	Local committee.
	COPELAND ISLANDS, Belfast Lough, N. Ireland.	Local committee.

In addition, observation and ringing stations were set up in 1956—57 on the islands of St. Agnes (Scillies), St. Kilda (Outer Hebrides), and Hilbre (Dee Estuary, Cheshire); at St. Catherine's Lighthouse (Isle of Wight); and in south-eastern England at Bradwell (Essex), Walberswick (Suffolk) and Sandwich Bay (Kent).

made. Also of importance is the careful identification of species which are either rare or difficult to determine, and the elucidation of fieldmarks so that such knowledge can be passed on to ornithologists in general (For examples, see ASH, 1956; WILLIAMSON and FERGUSON-LEES, 1955). This type of research, prompted by the critical nature of bird observatory work, has done much to raise the standard of field-identification and establish the sight-record as a reliable source of faunistic material. In consequence, trapping or careful field-identification have almost entirely replaced collecting as a means of establishing the occurrence of rare birds.

At Spurn and Gibraltar Point, on either side of the Humber Estuary, day-watches of »visible migration» and the effects of »lines of concentration» on incoming flocks are being closely studied, and sea-watches at Portland Bill have greatly improved our knowledge of sea-bird movements in the Channel region (ASH and ROOKE, 1954). At a number of stations intensive studies of the breeding populations, on a long-term basis, have been undertaken, the best-known instances being the studies of Manx Shearwater *(Procellaria puffinus)* and Storm Petrel *(Hydrobates pelagica)* at Skokholm (LOCKLEY, 1942, 1953; DAVIS, 1957), and of the Great Skua *(Catharacta skua)* and Arctic Skua *(Stercorarius parasiticus)* at Fair Isle. Skokholm was also the scene of investigations into the navigational ability of the Manx Shearwater (MATTHEWS, 1953).

Trapping and ringing have played a major role in bird observatory work. Heligoland traps of the kind described in detail by BROWNLOW (1952), often successfully modified to suit the local conditions and terrain, have been the main stand-by for sampling migrant flocks, but since 1956 nylon mist-nets have come increasingly into use. In 1954 the 11 bird observatories then operating accounted for more than a quarter of the grand total of 114,000 birds ringed in the British Isles. From 1955—57 the proportion has declined somewhat owing to the wide use of mist-nets by individual ringers, but the observatories remain the most valuable and accessible training-centres for potential bird-ringers, and have done and continue to do a great deal towards increasing the efficacy of the ringing scheme by developing new trapping techniques. Bird observatory methods are fully described in a new British Trust for Ornithology publication, »The Bird in the hand», by R. K. CORNWALLIS and A. E. SMITH.

MIGRATION THEORY

Critical analysis of the movements recorded by the bird observatories, in relation to the varying weather conditions over the Continent of Europe and the North Sea, has revolutionised our thinking in regard to the nature of the spring and autumn flow of migration through the British Isles. A decade ago the view was universally held that Britain lay athwart a trunk-route of migration used by many species of North European birds when travelling between their nesting-grounds and winter quarters (see CLARKE, 1912). In the early 1950's research at Fair Isle showed that this view was misleading, and that the vast proportion of Continental passage — of nocturnal migrants especially — through that isle and at other points along the east coast, is entirely adventitious and due to displacement on easterly winds from the narrow Skagerrak sea-crossing and the coastal »leading-lines» extending from Denmark southwards to northern France (WILLIAMSON, 1952). This »migrational drift» hypothesis stimulated parallel research at other bird observatories, and the analyses since published by CORNWALLIS (1954—56), JENKINS (1953), REDMAN and HOOKE (1954), DAVIS (1954) and DAVIS and WEAVING (1955—56), as well as from the Fair Isle observatory, have shown how general and ubiquitous is this phenomenon in western Europe.

The concentration of study on the meteorological background to migration has led to a clearer understanding of those factors of the external environment which promote, or inhibit, migration. The effects due to the movement of fronts in the North Sea region are evident from the papers mentioned, and are now well understood. Experience at the observatories has further shown that periods of anticyclonic or cool weather in the presumed area of origin of the birds, or linking that area with the British Isles, are coincidental with the big influxes noted in spring and autumn; and this has led to greater importance being attributed to the light strength of the wind (*i. e.* relative absence of factors promoting excessive drift) than to changes in

temperature and barometric pressure *per se* (WILLIAMSON, 1955). Indeed, the results of bird observatory work stress that this feature of the external environment, coupled with good visibility to permit visual contact with »leading-lines», is vital to the successful prosecution of a migratory flight.

There followed naturally from these discoveries a desire to extend the correlation between modern weather theory and observed migratory phenomena to the annual immigration of birds from Iceland and Greenland, and the vagrant arrivals from eastern North America. A cyclonic down-wind approach to Britain on the part of geese, waders and passerines nesting in Greenland and Iceland has been demonstrated (WILLIAMSON, 1953 etc.; WILLIAMSON and DAVIS, 1956), and in this connection the present author (1958 a) has shown that in interpreting the effect known as Bergmann's Rule »migrational drift» has an important evolutionary significance. The now generally accepted probability of fast down-wind flights across the North Atlantic storm-track has completely changed the trend of opinion concerning the admission of American vagrants to the British List (see *Ibis, 98:* 156), for »migrational drift» is regarded as a more plausible explanation of their regular appearance in Europe than the idea of »assisted passage» on Atlantic shipping advanced in the past (WILLIAMSON, 1954 c; ALEXANDER and FITTER, 1955).

FAUNISTIC WORK

On the faunistic side, it is of interest to note that of the 26 additions made to the British List since the end of the war, more than half have been reported by the bird observatories, as shown in Table 2. Of these no fewer than 7 are Nearctic forms, and this, together with the fact that all but one of the 7 Palaearctic forms have a central or eastern Asiatic distribution, fits well with the hypothesis that vagrant occurrences are due to »migrational drift».

The combined work of the observatories has shown, moreover, that many species formerly thought of as scarce vagrants are in fact fairly regular annual drift-migrants to our shores. The Yellow-browed Warbler *(Phylloscopus inornatus)*, Barred Warbler *(Sylvia nisoria)* and Red-breasted Flycatcher *(Ficedula parva)* are the most outstanding examples, but there are also the Scarlet Grosbeak *(Carpodacus erythrinus)* and Icterine Warbler *(Hippolais icterina)* in the north and east, and the Melodious Warbler *(H. polyglotta)* and Woodchat Shrike *(Lanius senator)* in the south and south-west. It is likely that the increasing reports from observatories of the Greenish Warbler *(Phylloscopus trochiloides viridanus)* and Red-headed Bunting *(Emberiza bruniceps)* reflect current attempts at a westwards expansion of range.

On the regional level there has had to be a considerable revision of the status of many birds. Perhaps the most striking example comes from Ireland, where work at Great Saltee Bird Observatory, off Co. Wexford, has shown that the Tree Pipit *(Anthus trivialis)* and Pied Flycatcher *(Ficedula hypoleuca)* — formerly considered

TABLE 2

Additions to the British List recorded by the Bird Observatories, 1948—57

Species or Sub-species	Bird Observatory	Date	Reference
Bonelli's Warbler, *Phylloscopus bonelli.*	Skokholm, Pembs.	31st August 1948	Conder and Keighley, *Brit. Bds., 42:* 215—6.
Isabelline Shrike, *Lanius isabellinus.*	Isle of May, Forth.	26th September 1950.	Alexander, Flower and Kinnear, *Brit. Bds., 44:* 217—9.
American Robin, *Turdus migratorius.*	Lundy, North Devon.	25th October-8th November 1952.	Davis, *Brit. Bds., 46:* 364—7.
Gray-cheeked Thrush, *Hylocichla minima.*	Fair Isle, Shetland.	5th—6th Oct. 1953.	Williamson, *Bull. F.I.B.O., 2:* 1—8; *Scot. Nat., 66:* 18—20; *Brit. Bds., 47:* 266—7.
Stilt Sandpiper, *Micropalama himantopus.*	Spurn Point, East Yorks.	31st August-4th September 1954.	Chislett, *Brit. Bds., 48:* 18—20.
Yellow-headed Wagtail, *Motacilla citreola.*	Fair Isle, Shetland.	20th—24th Sept. & 1st October 1954.	Williamson, *Bull. F.I.B.O., 2:* 191—3; *Brit. Bds., 48:* 26—9.
Baikal Teal, *Anas formosa.*	Fair Isle, Shetland.	30th September 1954.	Williamson, *Bull. F.I.B.O., 2:* 194.
Siberian Thrush, *Turdus sibiricus.*	Isle of May, Forth.	2nd October 1954. 1954.	Andrew, Nelder and Hawkes, *Brit. Bds., 48:* 21—5.
Yellowthroat, *Geothlypis trichas.*	Lundy, North Devon.	4th November 1954.	Whitaker and Eds., *Brit. Bds., 48:* 145—7.
Ring-necked Duck, *Aythya collaris.*	Slimbridge, Glos.	12th—14th March 1955.	Scott, *Brit. Bds., 48:* 377—8.
Hudsonian Whimbrel, *Numenius phaeopus hudsonicus.*	Fair Isle, Shetland.	27th—31st May 1955.	Williamson and Thom, *Brit. Bds., 48:* 379—81.
Thick-billed Warbler, *Phragamaticola aedon.*	Fair Isle, Shetland.	6th October, 1955.	Williamson *et al., Brit. Bds., 49:*
Steppe Shrike, *Lanius excubitor pallidirostris.*	Fair Isle, Shetland.	21st September 1956	Williamson, *Brit. Bds., 50:* 246—9.
Summer Tanager, *Piranga rubra.*	Bardsey, North Wales.	11th—25th Sept. 1957.	Condry, *Country Life,* 28th Nov. 1957: 1144—5.

great rarities — are regular on passage in small numbers (Browne and Ruttledge, 1957). A general study of the status of migratory species at Spurn Point, Yorkshire, has recently appeared (Chislett, 1958).

FIELD TAXONOMY

Formerly, taxonomic studies were the special province of the museum worker, using preserved material. Recent advances in systematics have stressed the importance of a consideration of biological phenomena, and it is now recognised that

migratory behaviour plays a considerable part in subspeciation (SALOMONSEN, 1955). The bird observatory, handling as it does a large amount of living material, is well placed to take a leading part in future taxonomic discoveries, and the extent to which the new technique of »field-taxonomy» can be developed and used to isolate different populations in bird-migration studies needs to be fully explored.

This approach has been a marked feature of the work at Fair Isle, which is particularly well placed for investigation of this kind because of its exposure to drift-movements from the Continent of Europe in the east, and to immigration into Britain from Iceland and Greenland in the north-west. A comparison of museum skins with trapped birds was first used in a study of the late autumn passage of Chiffchaffs *(Phylloscopus collybita)* (WILLIAMSON, 1954 a), leading to conclusions with regard to the intergradation of the races *abietinus* and *tristis* which were later confirmed by the museum work of HOLGERSEN and VOOUS (1955). Taxonomic data had already been used in an effort to isolate various migratory populations when the pattern of spring migration of the Willow Warbler *(Ph. trochilus)* through the British Isles in 1952 was revealed through an analysis of the mean weights and wing-length measurements of series trapped at a number of bird observatories (WILLIAMSON and BUTTERFIELD, 1954). This promising line of enquiry needs to be extended to other common species, while it would be of undoubted value to make repeat studies of the same bird or birds over a succession of seasons.

Perhaps the most successful applications of »field-taxonomy» to date have concerned the migratory behaviour, and relative status in Britain, of the Continental and north-western populations of certain species. The discovery at Fair Isle of an autumn passage of two distinct forms of the Merlin *(Falco columbarius)*, separable on wing-length, led to the acceptance of the large Icelandic race *subaesalon* by the B.O.U. Taxonomic and Records Committees, and established this as a key species in the study of the meteorological environment of migratory movements originating in Iceland and Greenland (BUTTERFIELD, 1954; WILLIAMSON, 1954 b). Subsequently, by a co-operative endeavour, a similar approach was used to fortify an analysis of the big invasion of Lapland Buntings *(Calcarius lapponicus)* which took place in autumn 1953, WILLIAMSON and DAVIES (1956) using data supplied by the bird observatories at Lundy, Skokholm, Fair Isle and a temporary station at Inishtrahull, off north-west Ireland, to show that the birds had close affinity with the dark, large-billed *subcalcaratus* inhabiting low-arctic Greenland. There was a strong indication in the evidence gained from museum study, however, that certain older invasions, affecting particularly south-east England, had a Continental source; and this seems to be confirmed by an investigation now being made of the big invasion reported by south and east coast bird observatories in 1956.

Taxonomic assessment of trapped birds, using criteria of weight and measurement as well as plumage characteristics, enabled the Fair Isle observatory to report on the meteorological conditions under which influxes of the Greenland low-arctic Redpoll *(Carduelis flammea rostrata)* take place into the Scottish isles, in some years in

abundance (WILLIAMSON, 1956). A mass of data collated at Fair Isle and the east coast bird observatories over the past eight years, combined with knowledge gained from taxonomic comparison of trapped birds, has enabled us to compare directly the weather situations which bring migratory movements of Continental and Icelandic Redwings *(Turdus m. musicus* and *coburni)* into the British Isles (WILLIAMSON, 1958 b).

LABORATORY EXAMINATION OF TRAPPED BIRDS

At most bird observatories the standard measurements of length of wing, tail, bill and tarsus are noted for many of the birds captured in the traps. The samples examined are in many cases large enough to warrant statistical analysis; they are frequently an important adjunct to the study of geographical variation or sex discrimination within the species, and have already revealed the serious inadequacy for critical identification of the measurements (based on small series of skins) given in the standard European fieldguides and handbooks such as HARTERT (1910) and WITHERBY *et al.* (1938). Apart from a note on the Blackbird *(Turdus merula)* (BUTTERFIELD, 1955) little of this information has yet been analysed, but now that a co-ordinating officer has been appointed for the bird observatories this information should soon be made available for wider use.

A number of bird observatories record bird weights. At present, our knowledge of the range and the causes of variation in most species is slight, though clearly diurnal and seasonal cycles are involved, and there are often sex and age-group differences. The complexity of the subject has been discussed by BLAKE (1956). The bird observatories are in an excellent position to make great contributions in this field, and an important paper published from Skokholm Bird Observatory by BROWNE and BROWNE (1956) is a valuable step in this direction. A vast amount of data, covering numerous species at different seasons, is awaiting collation and statistical treatment, and much of this may throw important light on biological problems. Work at Fair Isle and the Isle of May has revealed an important relationship between weight-loss and recent migrational history, with substantial recovery in the case of birds remaining »off-passage» for a period in a congenial environment. In the latter category a considerable amount of data, concerning mainly »off-passage» Chaffinches *(Fringilla coelebs)* and Bramblings *(F. montifringilla)* has been gathered at the Isle of May (BRYSON, 1951), and it is hoped to pursue further studies of this kind. The potential value of such data in migration analysis is adumbrated in notes by BUTTERFIELD (1952).

The moult of several species has been studied at Fair Isle through the examination of trapped birds, though only the Wheatear *(Oenanthe oenanthe)* and Crossbill *(Loxia curvirostra)* have yet been reported on (WILLIAMSON, 1957 a, b). There and elsewhere the composition by age and sex of migratory flocks has been investigated, a notable contribution to this being the current work at Spurn Bird Observatory on wintering flocks of Snow Bunting *(Plectrophenax nivalis)*.

A device designed as the result of experience at Fair Isle, and now used also at other bird observatories, has made possible for the first time quantitative as well as qualitative studies of the infestation of different host-species, at different ages and seasons, by ectoparasites such as fleas *(Siphonaptera)*, Hippoboscid flies *(Diptera)*, mites *(Arachnida)* and *Mallophaga*. The apparatus is described in *British Birds, 47:* 234—5. At least two ticks, one Hippoboscid fly *(Lynchia falcinelli*, an African species), and several species of *Mallophaga* new to the British Isles have been taken at the bird observatories in recent years. At Fair Isle extensive collecting in this field has brought about a greatly improved knowledge of the distribution and breeding-biology of the common bird-fleas (ROTHSCHILD, 1955 and in press); whilst research on the Hippoboscid fly *Ornithomyia fringillina*, based partly on morphological examination and partly on the release and recapture on bird-hosts of colour-marked individuals, has produced a thorough ecological study of this important avian parasite (CORBET, 1956 a, b). Studies have also been carried out at Skokholm, but before all the ecological problems can be satisfactorily resolved intensive work along the lines established by CORBET needs to be conducted with bird-populations occupying other environments.

It will be seen that the work of the British bird observatories covers a wide field. Individually and collectively they have played an important part in improving our knowledge of migration through, and within, the British Isles. Now that a research officer has been appointed by the British Trust for Ornithology to assist and co-ordinate their activities, the observatories' contribution to bird-migration and allied problems should greatly increase in the years ahead.

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Role of Light and Darkness in the Regulation of the Annual Stimulus for Spring Migration and Reproductive Cycles[1]

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INTRODUCTION

Experimental studies of the regulation of migratory behavior were initiated by ROWAN (1925, 1929), who discovered that gonadal recrudescence could be induced out of season, in late fall and winter, by subjecting Slate-colored Juncos *(Junco hyemalis)* to artificial increases in day length. On the assumption that migratory behavior in the spring was a phase of sexual behavior, ROWAN tested the effect of experimentally induced gonadal recrudescence on migratory behavior by releasing juncos in winter, many months ahead of the normal time of their spring migration, with their gonads at various stages of development. From the results of these experiments, ROWAN concluded that in the Slate-colored Junco, and other fringillids, the stimulus to migrate in the spring was regulated by external and internal factors. The external factor was the increasing day length after December 21. The internal factor was the production of sex hormones, which he correlated with the recrudescing gonads of spring and the regressing gonads of fall. The minimal gonad of winter and the maximal gonad of the breeding period showed little or no hormone-producing interstitial tissue, and, hence, would not stimulate migratory behavior. From the results of later work with crows *(Corvus brachyrhynchos)* ROWAN (1932) concluded that the southward migration in fall appeared to be independent of the influence of the gonads.

ROWAN's epochal work defined the basic problems and stimulated an experimental attack on the regulation of bird migration and gonadal cycles. The first extensive series of experiments which were designed to test ROWAN's hypothesis

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were performed by WOLFSON (1940, 1942, 1945) in Berkeley, California using the Oregon Junco *(Junco oreganus)*, a species closely related to the Slate-colored Junco. These experiments corroborated ROWAN's observation that birds could be stimulated to migrate northward months ahead of time by subjecting them to artificial increases in day length in the late fall and winter. However, they also demonstrated that birds in breeding condition would migrate, which was contrary to ROWAN's conclusion. WOLFSON found that in addition to gonadal growth preceding migration there was also a marked increase in body weight caused by large deposits of subcutaneous and intraperitoneal fat, which appeared to be a better criterion of a readiness to migrate than the condition of the gonad. Later studies demonstrated that the pituitary was also involved in this premigratory change in physiological state. Members of a non-migratory race of the same species, which were exposed to the same environmental conditions in nature and in the laboratory, differed from migratory individuals in not showing marked deposition of fat nor increase in body weight and in having a much faster rate of gonadal development which resulted in an earlier breeding season.

The experiments of ROWAN and WOLFSON pointed clearly to the increasing day lengths of winter and spring as the environmental timer for spring migration, but there was a serious weakness in this aspect of ROWAN's theory. Birds that wintered in the north temperate zone or northern subtropical zone would experience substantial increases in day length after December 21, but not the birds which wintered in the tropics, on the equator, or in the southern hemisphere. In the northern tropics the increases in day length would be slight; in the equatorial region there would be practically no change; in the southern hemisphere, the birds would arrive in November when the days were increasing in length, and after December 21 the days would decrease in length until spring migration was underway in March and April. Increasing day length, obviously, was not a feature of the environment on the wintering grounds of all migratory birds.

To overcome this weakness of ROWAN's theory, BISSONNETTE (1937), on the basis of his studies of the gonadal cycle of the Starling *(Sturnus vulgaris)*, postulated that there was an inherent rhythm of activity of the pituitary gland. Birds migrated southward due to regression of pituitary activity and did not breed on the wintering grounds because the pituitary and gonads were in a refractory phase. On the spontaneous recovery of the pituitary in late winter or spring, the birds were stimulated to migrate before or while the gonads recrudesced. BISSONNETTE's theory precluded any regulatory effect by day length in the tropics and southern hemisphere.

Although there was ample experimental evidence for the existence of a »refractory period» in the fall when increasing day lengths would not stimulate gonadal growth, it seemed to me that if day length played a regulatory role in north temperate species, that it might play a similar role in species that winter in the tropics and southern hemisphere. Since the days were not increasing in length in those areas, perhaps some other aspect of »day length» was operating. Possibly the summation of the daily amounts of light was important and not whether the day lengths were

increasing, decreasing or constant. If a given amount of light each day produced a proportional increment of physiological response, then the timing of spring migratory behavior could conceivably be determined by the summation of the daily amounts of light and the concomitant summation of the daily proportional physiological increments to a threshold. This hypothesis was put forth as the »summation hypothesis» (Wolfson, 1947). The research in my laboratory during the past ten years has been concerned primarily with the nature and regulatory role of day length and with certain aspects of the change in physiologic state which precede spring migration — body weight, fat deposition, and gonadal activity. Excellent reviews of the published literature on various aspects of the fundamental problems have appeared recently (Burger, 1949; Galgano and Mazzi, 1951; Hammond, 1954; Wallgren, 1954; Aschoff, 1955; Wagner, 1956; Weise, 1956; King, 1957; Rautenberg, 1957; Farner, 1955, 1959; Wolfson, 1952 a, 1959 a). Consequently, in this paper I shall summarize primarily the unpublished studies and other relevant data from our laboratory, with particular emphasis on the qualitative aspects. More detailed and quantitative analyses of these studies will appear later elsewhere.

DAY LENGTH AND PROGRESSIVE PHASE OF THE MIGRATORY AND REPRODUCTIVE RESPONSES

The first test of the summation hypothesis was the determination of the amount of light which migratory birds wintering at various latitudes received under natural conditions (Wolfson, 1952 a). These data showed only small differences in the summations from December 21 until the onset of migration in March or April. Hence, experimental studies were begun to test the hypothesis.

Two species have been used extensively in our laboratory, the Slate-colored Junco and the White-throated Sparrow *(Zonotrichia albicollis)*. Both are temperate zone species and migrate through Evanston in spring and fall. Evanston is also within the wintering range of the junco. Occasionally other species are used in addition. In most of the experiments which will be described the attainment of the spring migratory state was determined by observations on body weight, fat depots, and gonadal recrudescence. This state can be easily recognized in live birds by means of changes in body weight and observations of the fat depots. In a few experiments birds were released to determine their behavior. Data were obtained also on other phases of the annual gonadal cycle. That the premigratory physiological state is a good indicator of a readiness to migrate has been demonstrated by studies of migratory restlessness (Zugunruhe) in caged birds (Eyster, 1954; Farner, 1955, review; Weise, 1956).

If summation of daily responses were a regulatory factor, and if the daily responses were proportional to the amount of light, then wintering birds subjected to different daily doses of day length should show differences in time of response,

with those receiving the most light in a given period of time, responding first. The cumulative action of daily photoperiods had been considered earlier in relation to the testis cycle of nonmigratory Starlings (BURGER, 1939 a, 1939 b, 1940) and House Sparrows *(Passer domesticus)* (BARTHOLOMEW, 1949) and the molt cycle in the the tropical weaver finches *(Euplectes, Vidua, Steganura)* (BROWN and ROLLO, 1940). The results of these investigations showed clearly the importance of the daily photoperiod and the existence of threshold values for stimulation and inhibition.

In the first series of experiments (WOLFSON and WINN, 1948; WINN, 1950) birds were captured during the fall migration and were subjected to the following constant daily periods of light and darkness beginning December 4: 9L—15D; 12L—12D; 15.5L—8.5D; 20L—4D; 24L. One group of birds was also maintained under natural day lengths. This experiment was conducted twice, but adequate gonadal data were obtained only during the second experiment. The fat deposits which are diagnostic of the premigratory physiological state occurred in all of the groups and in a definite sequence. Figure 1 shows the normal period of fat deposition and concomitant increase in body weight in captive birds held under natural day lengths. Figure 2 compares the time of onset of fat deposition and duration of fat deposits in all the groups and in both experiments. The response of the testis also occurred in a sequence. Figure 3 shows the growth of the testis under natural day lengths and figure 4 compares the responses in all of the groups. Not only did the time of occurrence of fat

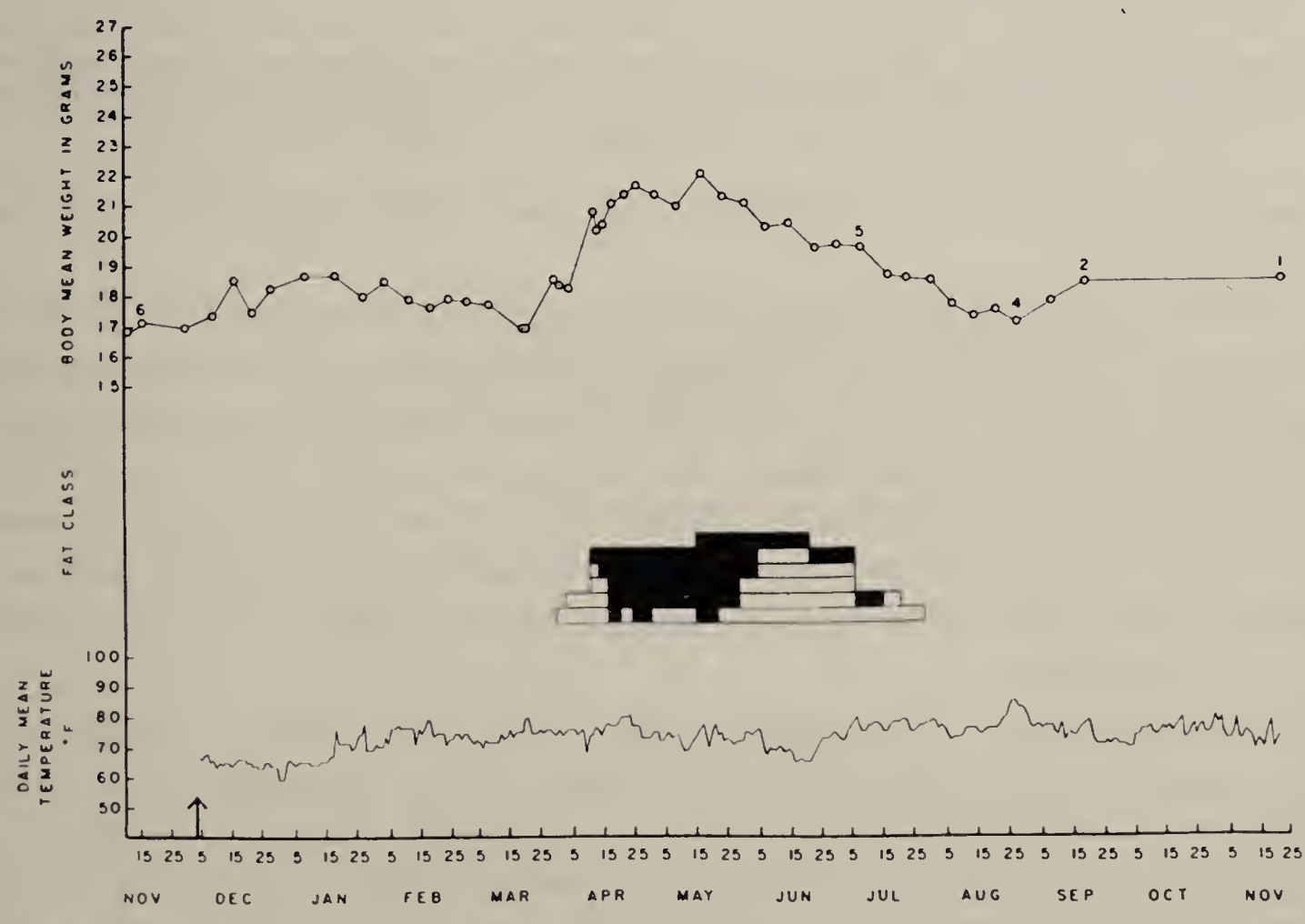

Fig. 1. Fat deposition and body weight in the Slate-colored Junco under natural day lengths beginning December 4. The numbers above the points in the curve of body weight indicate the number of birds. For fat response, blackened areas represent birds in the heavy fat class, white areas those in the moderate class, for each date of weighing. The number of individuals in each fat class is indicated by the height of the column, each rectangle representing one bird.

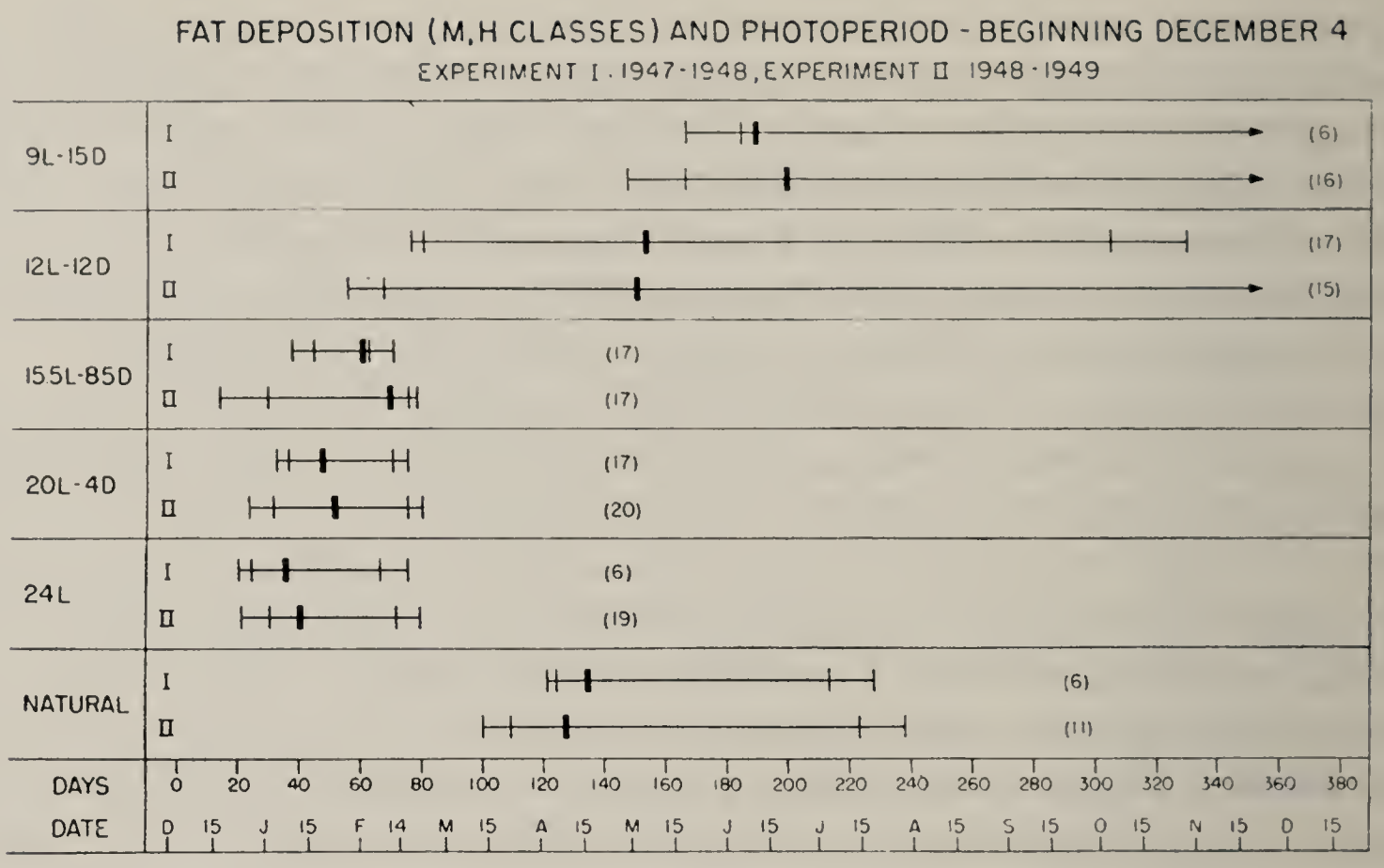

Fig. 2. Time of fat deposition (medium and heavy classes) in relation to photoperiod, beginning December 4. Upper horizontal bar in each photoperiod represents experiment I, the lower one experiment II. Numbers at the right of each bar indicate the numbers of birds at the beginning of the experiment. The first vertical line at the left of each bar indicates the time at which 30 per cent of the individuals showed medium and heavy fat deposits; the second line indicates 50 per cent response. The heavy black vertical bar indicates the time of the highest percentage of response. Vertical lines at the right end of the bar indicate the loss of fat deposits, the first bar for 50 per cent of the birds, the end one for 30 per cent. An arrowhead at the end of the bar indicates that the fat deposits were not lost in 50 per cent of the individuals. (Data from WINN, 1950).

deposits and of maximal testes differ, but also the duration of fat deposition and of spermatogenesis.

The results of these experiments showed clearly that the duration of the daily photoperiod (in a 24-hour cycle) determined the time when the premigratory physiological state occurred and when the testis reached complete spermatogenesis. In relation to ROWAN's original theory, the significant results were a) that constant day lengths, even when as short as 9 hours and without increase from the shortest winter days to which the birds are subjected in nature, induced fat deposition and gonadal growth and b) that there is a relation between length of day (photoperiod) and rate of response.

The interpretation of the results of these experiments and the earlier ones of ROWAN and WOLFSON was as follows (WOLFSON, 1952 a): The daily photoperiod — whether constant or increasing gradually — induces an »increment of physiological change.» The magnitude of the increment is proportional to the daily photoperiod and it appears to be near the maximum at 16 hours in a 24-hour cycle. The minimum is not known, but it is apparently less than 9 hours. The daily increments of physiological change summate and regulate the time the responses occur and the rate at which they proceed. To determine whether birds held at the minimal winter day length of

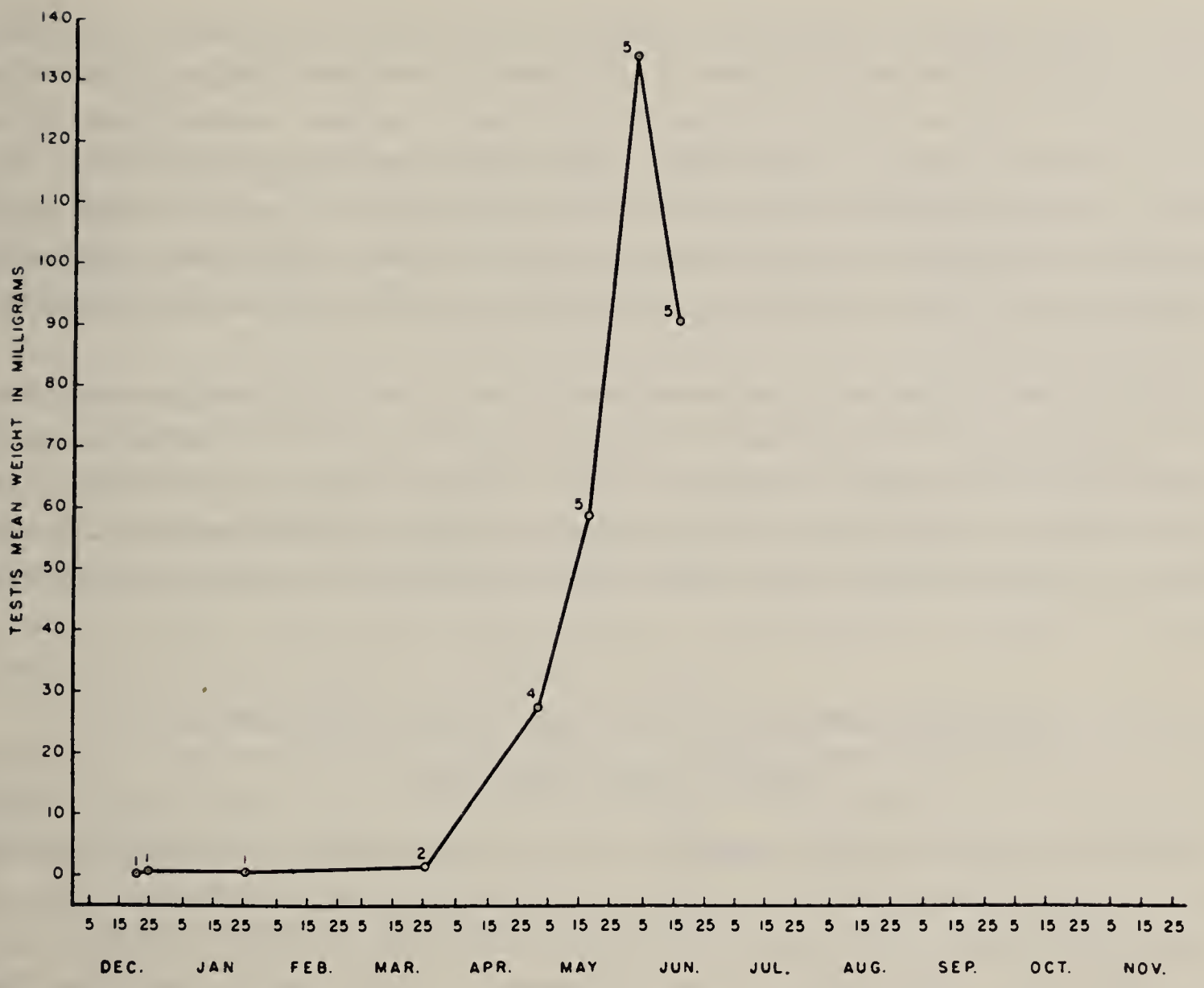

Fig. 3. Weight and development of testis in the Slate-colored Junco under natural day lengths beginning December 4. The numbers above each point indicate the stage of spermatogenesis (Wolfson, 1942). Each point represents one individual. (From Winn, 1950).

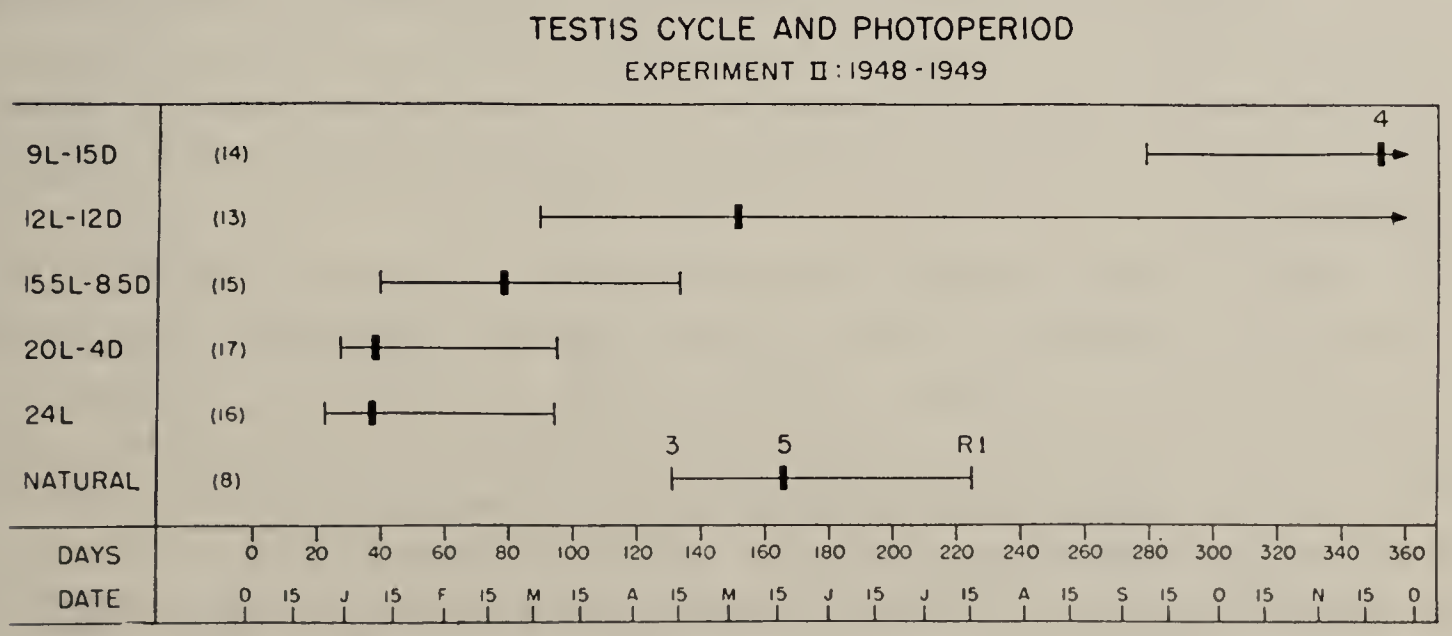

Fig. 4. Testis cycle in relation to photoperiod. Numbers at left of horizontal bars indicate the number of birds at the beginning of the experiment. Key to the vertical lines is shown on the bar for birds treated with natural day lengths. Stage 5 is the stage of complete spermatogenesis. R1 indicates regression to minimum condition. Arrowhead at right end of bar indicates that no regression occurred during the period shown. (Data from Winn, 1950).

9 hours would migrate, birds were released in early June in a recent experiment (1957). Both White-throated Sparrows and juncos were used. Although there was considerable variation in fat condition at the time of release, about 60 percent of the birds left the area and presumably migrated. It would appear, therefore, that increases in day length in winter are not necessary for the occurrence of spring migration. Day lengths in winter merely govern the rate at which the premigratory state develops and, hence, when spring migration occurs. They do not control whether or not it will occur.

On the basis of the results obtained in the junco and the interpretation given above, day length could regulate the onset of migration in birds wintering in the tropics and in the southern hemisphere. Even though the days are constant on the equator and are decreasing in the southern hemiesphere after December 21, they could be above the length of the daily effective photoperiod for the birds wintering there.

DAY LENGTH AND THE MAINTENANCE OF THE MIGRATORY AND REPRODUCTIVE RESPONSES

This first series of experiments demonstrated primarily a relation between the duration of the photoperiod in a 24-hour cycle and the time of initiation of the fat and gonadal responses. Was there also a relation between the daily photoperiod and the maintenance (or duration) of these responses once they had begun? If so, then the daily photoperiod would be a highly significant factor in the regulation of the entire annual cycle and not just the initiation of spring migration and the breeding cycle. Some relevant data were available from the previous series of experiments, but a new series of experiments was designed specifically to answer this question. Birds were caught during the spring migration in April and May and subjected to constant day lengths of 9, 12, and 20 hours (photoperiods in a 24-hour cycle), and to natural day lengths. At the beginning of the experiment the gonads were partly developed, and the birds showed also heavy fat deposits indicative of the migratory physiological state.

The results of these experiments were generally in accord with those of the previous series in showing a relation between the daily photoperiod and the rate, extent, and duration of response. However, there were also some differences. In the 9-hour group the gonads regressed almost immediately. In the previous experiment it was shown that a gonadal response could be induced eventually with a constant 9-hour photoperiod, yet in this case regression occurred. In the present experiment the testes were in an advanced condition correlated with the natural day lengths of approximately 14 $^1/_2$ hours at the start of the experiment. When the day length was reduced to 9 hours, perhaps the daily increment of gonadal stimulus was too small to meet the demands of the partly enlarged testis. Was the reduction in day length as such responsible for the regression in the 9-hour group? Probably not,

for in the 12-hour group, which experienced a reduction in day length (from natural conditions) of approximately 2 $^1/_2$ hours at the start of the experiment, gonadal growth continued.

In the natural and 20-hour groups the gonads regressed (with one exception) after a few months of activity, as occurs in nature. In the 12-hour group activity of the testes was maintained for about nine months; in the previous experiment no gonadal regression was observed up to one year after the start of the experiment. Fat deposition continued in all of the groups, but the fat deposits disappeared first in the 9-hour group. The largest fat deposits were seen in the 12-hour group. The deposits disappeared (with one exception) in the natural and 20-hour groups before they molted, but most of the birds in the 12-hour group retained their fat deposits for many months and failed to molt. Figure 5 shows the occurrence and duration of fat deposits, reproductive activity and molt under natural day lengths in a captive group of 21 birds. From similar curves, figure 6 was prepared to compare the same responses in groups exposed to different schedules.

In the experiment just described, treatment was of necessity begun on different dates as the birds were captured. Comparison of two groups treated with 12L,—12D beginning April 6 and April 16 is shown in figure 7. The difference in the gonadal cycle is striking. A possible explanation is the difference in the initial condition of

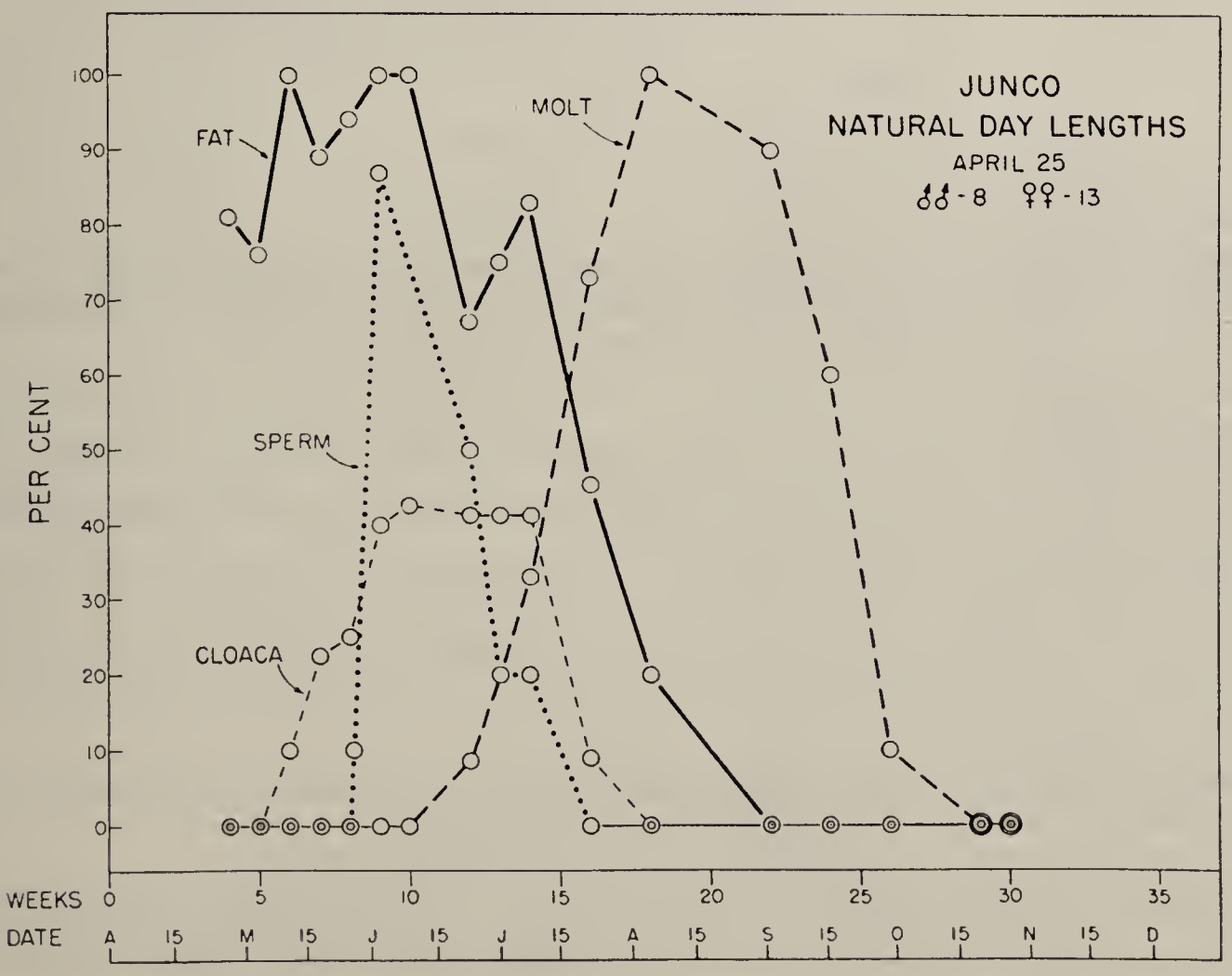

Fig. 5. Fat, reproductive, and molt responses in the Slate-colored Junco under natural day lengths. Response is indicated as per cent of occurrence in the 21 birds in the group, except for sperm where it is based on males only. The lower frequency of the cloacal response is due to the fact that it occurs primarily in males, but the percentage is given for the entire group.

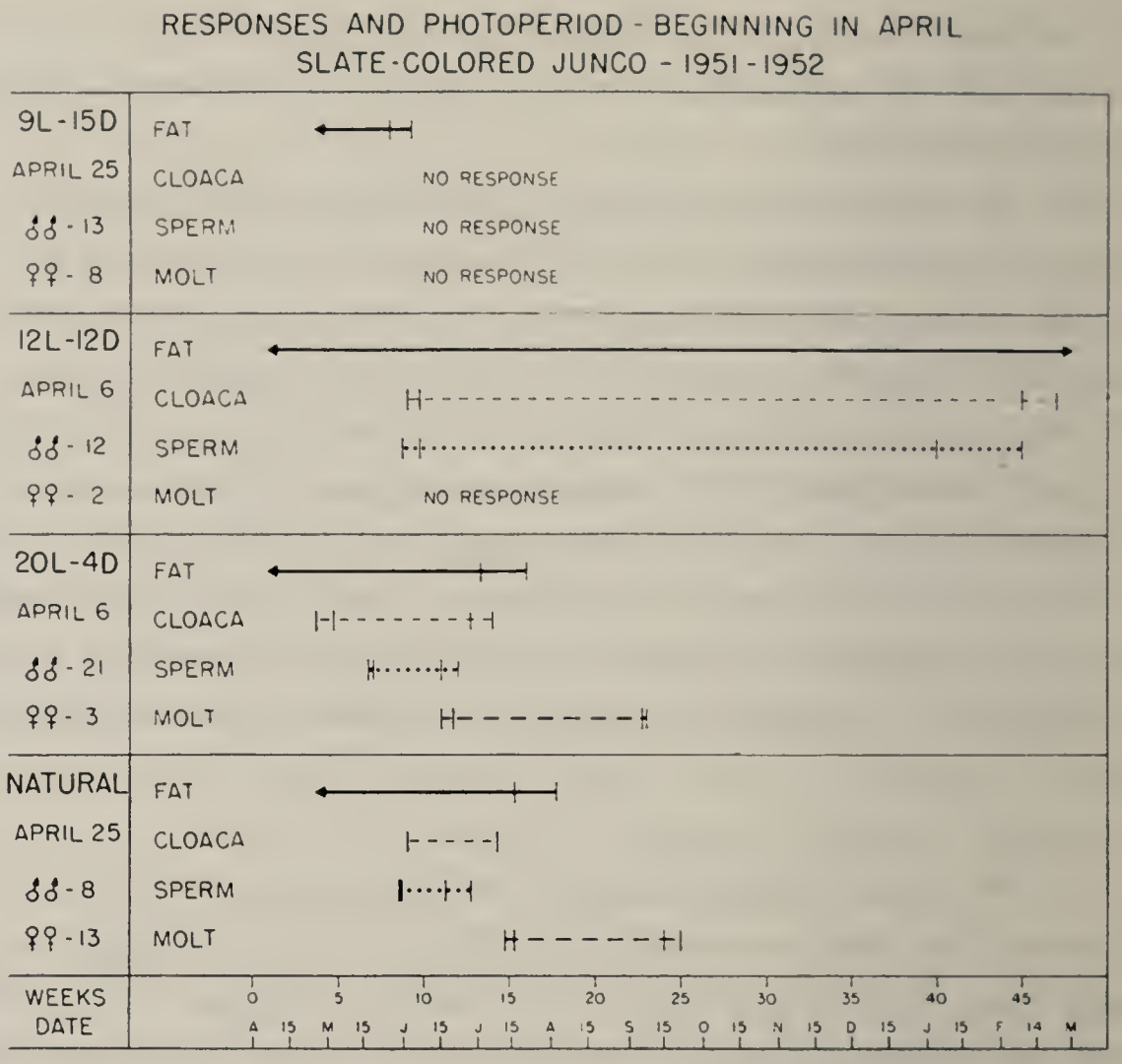

Fig. 6. Fat, reproductive, and molt responses in relation to photoperiod. For explanation of bars, see legend for figure 2. The only difference here is that the percentages used are 40 and 60, rather than 30 and 50 as in figure 2.

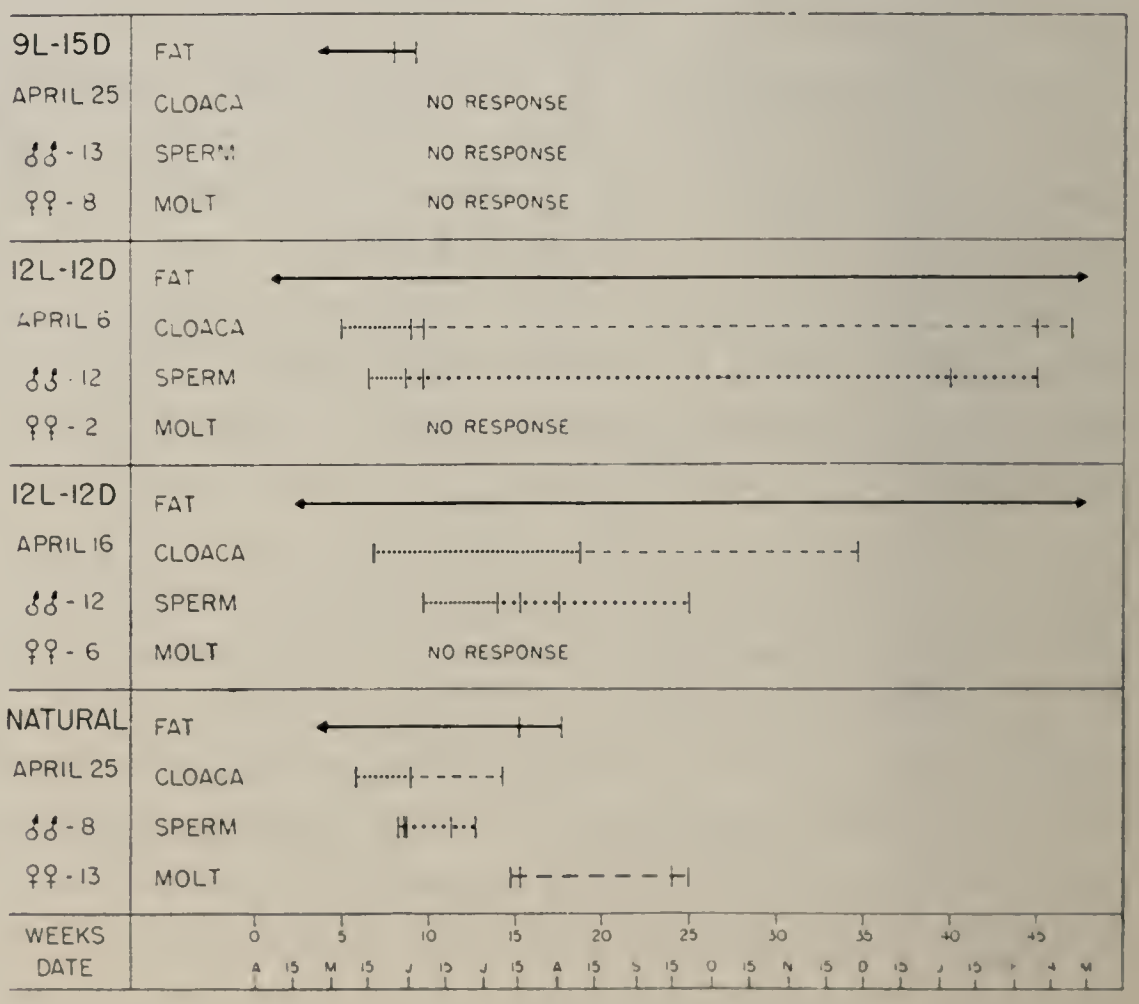

Fig. 7. Comparison of fat, reproductive, and molt responses in birds treated with 12L.—12D, beginning April 6 and April 16. Responses under 9L.—15D and natural day lengths are included for comparison. For explanation of bars, see figures 2 and 6. One addition here is the indication of the *initiation* of the cloacal and sperm responses, which is shown by the first vertical line at the left; small dots toward the right from this line stop at the 40 per cent response line.

the testes and the greater decrease in day length (from natural conditions) which the April 16 birds experienced (about one-half hour less than the April 6 birds).

Figure 8 compares birds treated with 20L—4D beginning April 6, April 17, and April 25. The general similarity in the response of these groups and the natural group suggests that the gonadal cycle is operating at close to its maximal rate by late April. However, the birds treated beginning April 6 seem to show a slight acceleration of the gonadal and molt cycles.

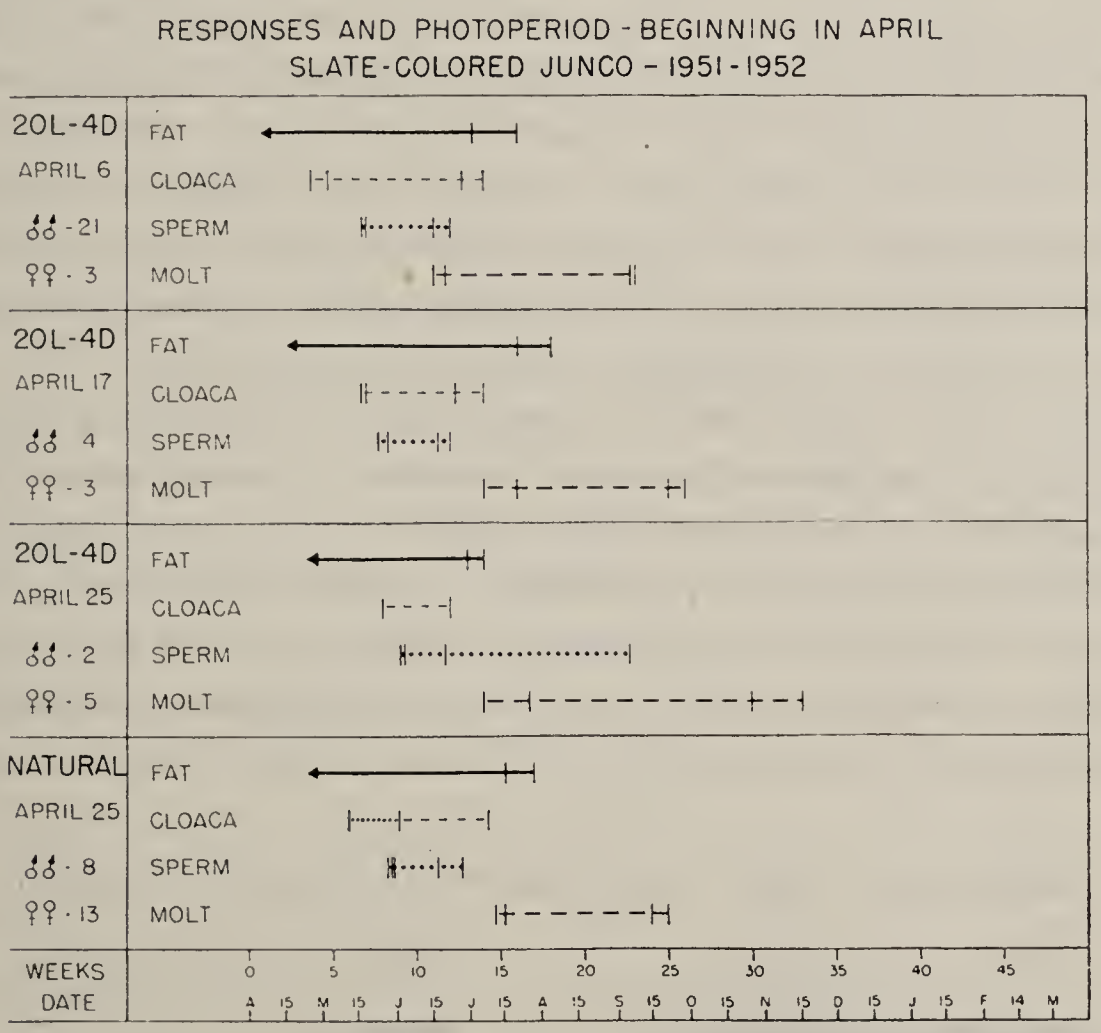

Fig. 8. Comparison of fat, reproductive, and molt responses in birds treated with 20L—4D beginning April 6, 17, and 25. Responses under natural day lengths are shown for comparison. For explanation of bars see legends for figures 2 and 6.

The results of the first series of experiments showed that the daily photoperiod determined the time at which the response occurs. The results of the second series demonstrated that the daily photoperiod regulates also a) the maintenance of the response, b) the rate at which the response proceeds, and c) the duration of the gonadal and fat cycles (or the time of gonadal regression).

ROLE OF LIGHT AND DARKNESS IN THE PROGRESSIVE PHASE OF THE MIGRATORY AND REPRODUCTIVE RESPONSES

At about the time the second series of experiments was concluded, KIRKPATRICK and LEOPOLD (1952, 1953) and JENNER and ENGELS (1952) demonstrated the importance of the dark period in the gonadal response to the daily cycle of light and darkness. In the studies in our laboratory described above none of the experiments had been designed to distinguish between the roles of light and darkness. Hence,

further experiments were undertaken to determine the role of the dark period in relation to the summation hypothesis.

If the effective stimulus is the amount of light which a bird receives daily, or in a given period of time, then birds receiving 20 hours of light per day in one dose or in four equal doses of 5 hours should respond equally well. In both cases the birds would receive the same total amount of light per 24-hour period. They would also receive the same ratio of light to darkness in each cycle. The only basic difference would be the length of each cycle. In the first experiment the birds were subjected to 5-hour photoperiods followed by 1-hour dark periods (5L—1D) (Wolfson, 1953). The results demonstrated clearly that a 6-hour cycle of 5L—1D was strongly stimulatory for the gonadal and fat responses (figure 9). The rapidity of response was similar to that in birds on a 20L—4D schedule, with a tendency toward a greater fat response and a greater reproductive response in the females.

These results were interpreted as supporting the summation thesis that the daily amount of light regulates the rate of response. However, since the proportion of light to darkness per 24 hours and per cycle was the same, there was the possibility that this proportion was the effective stimulus and not the daily dose of light. The work of Kirkpatrick and Leopold (1952, 1953) and Jenner and Engels (1952) pointed to the duration of the dark period in a 24-hour cycle as the regulatory factor in the daily schedule, but their experiments, which involved interrupting the

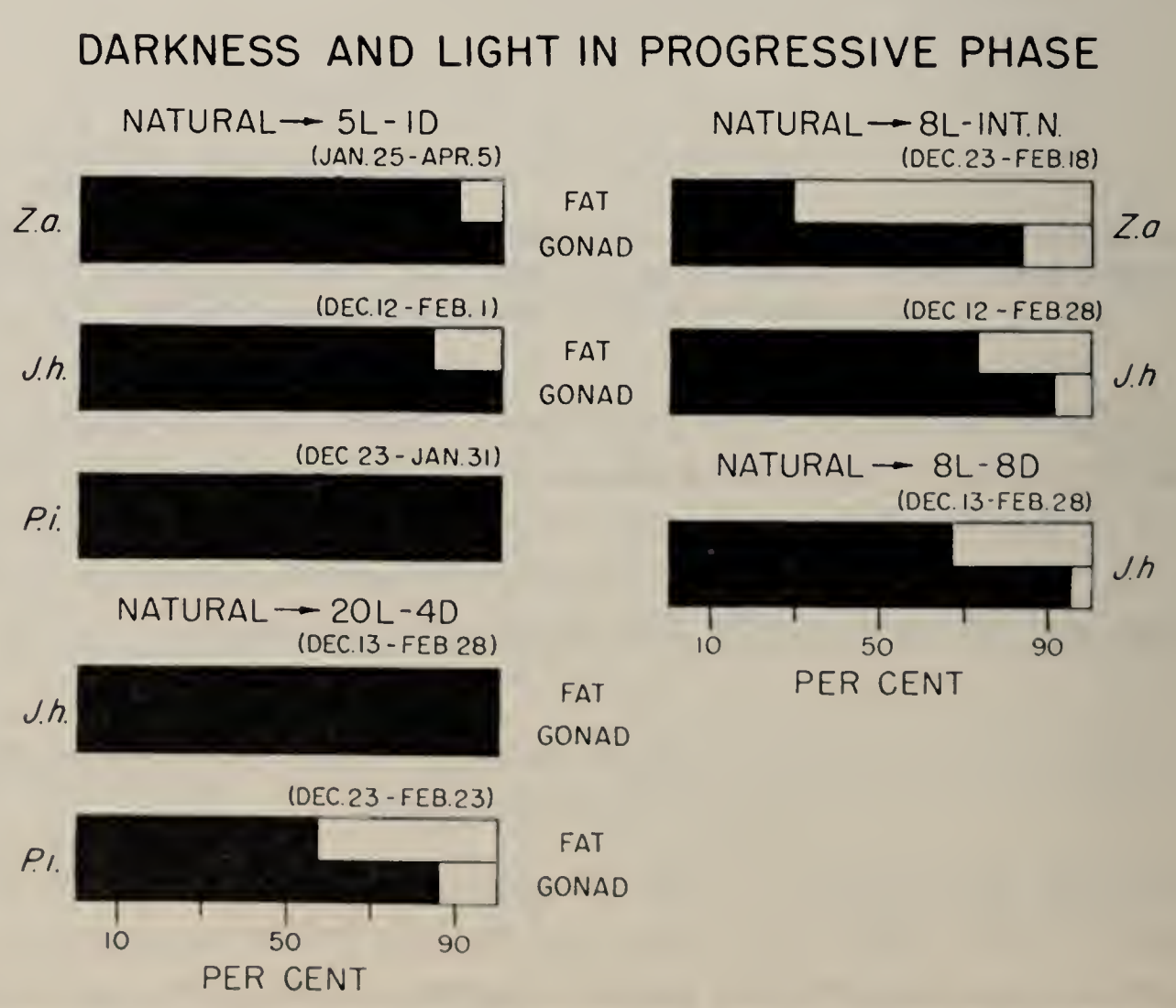

Fig. 9. Fat and gonadal responses under various schedules of light and darkness during the progressive phase. Response is indicated as per cent which showed each response. Abbreviations as follows: Z.a., *Zonotrichia albicollis;* J.h. *Junco hyemalis;* P.i., *Passerella iliaca.*

dark period with a brief period of light, did not rule out the proportion of light to darkness as the effective daily stimulus. For example, in the schedules used, 8.25L, 7D—1.75L—7D (JENNER and ENGELS, 1952) and 9L—7D—1L—7D (KIRKPATRICK and LEOPOLD, 1952) the first cycle of light and darkness in the 24-hour period was close to a 1: 1 ratio and the light period was longer. This could have been the effective cycle of the 24-hour period. The second cycle, with its much greater proportion of darkness might not have been stimulatory.

The next experiments in our laboratory involved the use of an interrupted night schedule and a related one to examine the role of the ratio of light to darkness. The schedules were as follows: 8L—7.25D—1.5L—7.25D and 8L—8D. In the first schedule, the 16-hour dark period was interrupted with 1.5 hours of light. In the second, the 8L—8D simulated the 8L—7.25D part of the interrupted night schedule. The birds responded similarly under both treatments (figure 9). Both of these schedules acted like the long days (15.5L, 20L) of the earlier series of experiments, yet the amount of light in a 24-hour period was only 9.5 hours in the interrupted night schedule. In the 8L—8D schedule, the amount of light alternated from 8 to 16 hours per 24-hour period. With a schedule of 8 hours or 9.5 hours of light per day in one dose in a 24-hour cycle, birds do not respond in eight or ten weeks.

The results of these experiments confirmed the work of KIRKPATRICK and LEOPOLD (1952) and JENNER and ENGELS (1952) and pointed to the length of the night or dark period in a 24-hour cycle as the regulatory part of the light-darkness schedules which induce photoperiodic responses. An alternative explanation was put forth by FARNER, MEWALDT, and IRVING (1953 a, 1953 b). They suggested that the daily dark period *per se* has no positive function, rather, there is a persistent carry-over period which follows the end of the photoperiod, and the effective part of a photoperiodic schedule is the photoperiod plus the carry-over period. They envisioned the carry-over period as having a duration of a fraction of an hour to several hours and as a probable function of the duration and nature of the preceding photoperiod. Rate of testicular response was interpreted as a direct function of the summated daily gonadotropic effects of the photoperiods and the carry-over periods. The interpretation of FARNER, MEWALDT, and IRVING was in agreement with the hypothesis of summation of daily physiological increments, but they suggested the carry-over period as an additional effective part of the photoperiodic cycle.

Digressing for a moment, I should like to point out in relation to this problem of the role of light and darkness that although the initial work in our laboratory showed a relation between rate of response and the daily photoperiod, the experiments were not designed to distinguish between the roles of the photoperiod, the dark period, or a relation between them, The summation hypothesis was stated originally in terms of the response to day lengths, or photoperiods, but it was pointed out that these terms were used only relatively. The role of the dark period in daily light-dark schedules will be discussed shortly, but I wish to distinguish here between the theory of summation of *daily* increments of physiological change in response to an effective

daily photoperiod schedule, over which there is no disagreement, and the role of light and darkness in the daily photoperiodic cycle, over which there is disagreement. The theory of summation, I must also point out, is only an interpretation at present; there is no objective evidence for it.

The results of the two experiments just reported were interpreted as demonstrating an inhibitory effect of a long dark period. But they also showed that the ratio of the durations of the light and dark periods in a given cycle might also be a factor in inhibition. The next experiment was designed to test the role of the ratio of light to darkness and to obtain data bearing on the existence of a carry-over period. The schedule chosen was 1L—2D and the experiment was performed twice. In each cycle there was the same proportion of light to darkness and the same total amounts as in the schedule of 8L—16D, which is not stimulatory. If the birds failed to respond, then it would seem unlikely that there was an effective carry-over period. All the birds showed a marked and rapid gonadal response (figure 10). The results demonstrated again that only a small total amount of light per day, in this case 8 hours, is highly effective when there is no long inhibitory period of darkness. Since the proportion of light to darkness in each cycle was non-stimulatory (1L—2D), and since the total amounts of light and darkness per day (8L and 16D) were also non-stimulatory, the positive results ruled out both of these as effective aspects of the daily photoperiodic cycle. They pointed instead to the effectiveness of small amounts of light per day when there was no long period of darkness, or to the existence of carry-over periods, depending on one's interpretation.

To examine further the possible role of a long period of darkness as an inhibitory factor, the pertinent experiments in the literature were examined and another experiment was performed in our laboratory. The experiments in the literature (Burger, Bissonnette, and Doolittle, 1942; Kirkpatrick and Leopold, 1952, 1953; Jenner and Engels, 1952; Farner, Mewaldt, and Irving, 1953 a, 1953 b; Kirkpatrick, 1955) showed that in most cases birds responded to »light periods» given either as flashes of light or when broken up with dark periods, as long as there was no single long dark period of about 14 hours duration in a 24-hour period. There were some exceptions. In some cases, the flashing »schedules» were not effective, for example, 5 sec.L—15 sec.D and .1 sec.L—5 sec.D (Burger, Bissonnette, and Doolittle, 1952). In the experiments of Farner, Mewaldt, and Irving (1953 a, 1953 b), the response was poor in some cases, but only with a schedule of 12.2L—11.8D was there a clear-cut failure to respond (9 out of 12 birds) when the duration of a continuous dark period was less than 14 hours. The other experiments which they reported and interpreted in terms of carry-over had no continuous dark periods long enough to inhibit the light periods. The experiments in the literature seemed to me to favor the interpretation of a long period of darkness as inhibitory, but there was also a basis for a carry-over effect of the photoperiod.

To test the effect of an inhibitory period of darkness following an effective series of light periods, the following schedule was used in the next experiment in

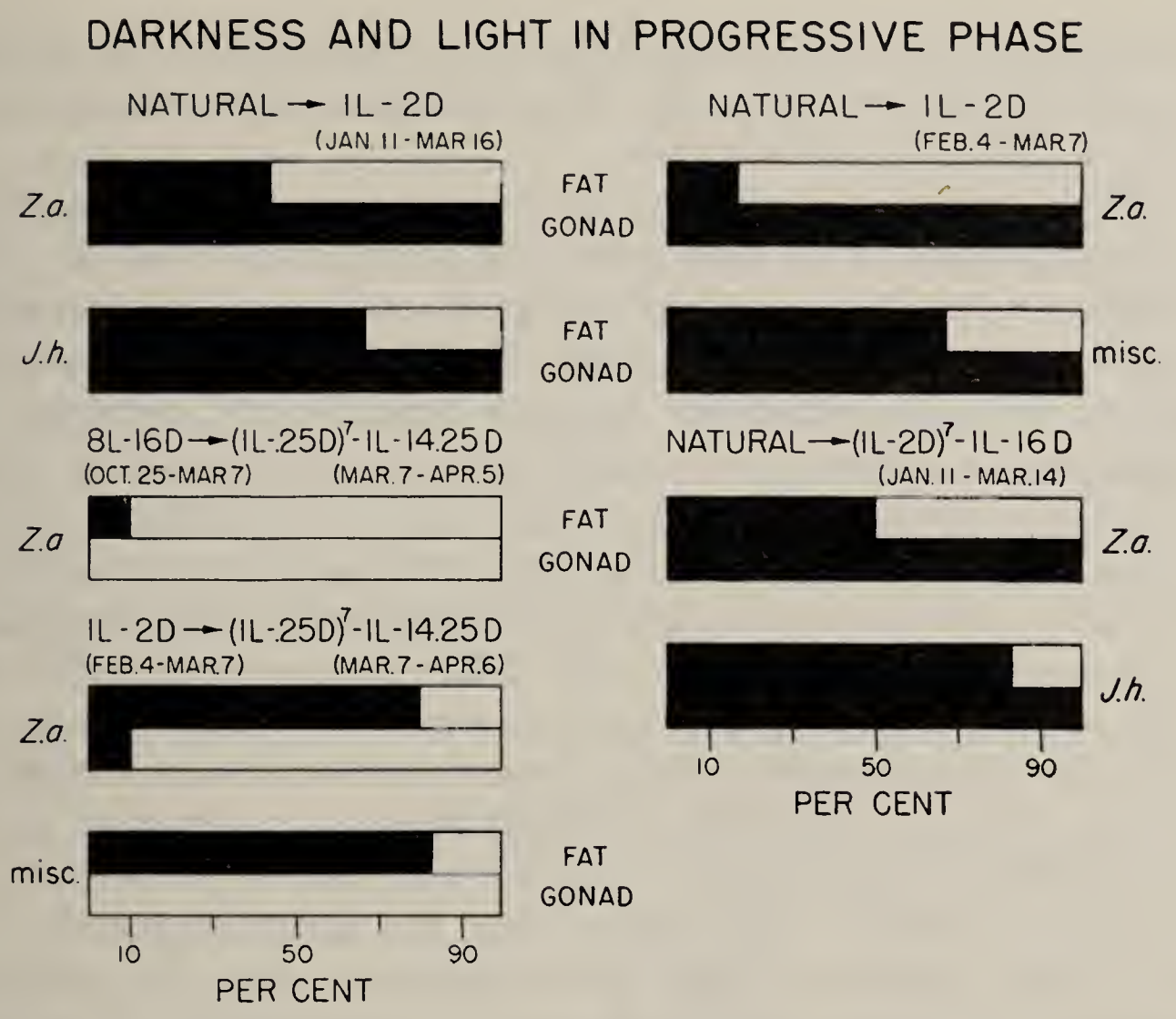

Fig. 10. Fat and gonadal responses under various schedules of light and darkness during the progressive phase. Abbreviations as in figure 9; misc. refers to a miscellaneous group of fringillids.

our laboratory: $(1L—.25D)^7—1L—14.25D$. This schedule provided eight 1-hour periods of light as in the 1L—2D schedule and a similar total of 8 hours of light in 24 hours. It differed in having only 15 minute dark periods interspersed among the 1-hour light periods and in having one long continuous period of darkness which was known to be inhibitory. The birds failed to respond, and this schedule not only failed to initiate a response, but also failed to maintain the reproductive condition of some birds which were already active at the beginning of the experiment (figure 10). These results can be interpreted as supporting the inhibitory role of long periods of darkness, and it is tempting to do so. It can also be argued that a 15-minute period of darkness did not allow enough time for the complete use of the carry-over periods of the 1-hour photoperiods and, hence, the effective photoperiods and carry-over periods could not exceed a total of about 10—12 hours. The data did not permit a clear-cut choice between these alternative explanations.

If a long dark period was inhibitory what would happen if such a period was used after a 1L—2D schedule? This was done with the following schedule: $(1L—2D)^7$ —1L—16D. All the birds showed a gonadal response. Since an effective period of light treatment was not inhibited by a known inhibitory dark period, these results demonstrated the importance of the light period as the effective stimulus. But this interpretation is also open to question. In this experiment the cycle was 38 hours

long. The effective light period, despite interruptions with dark periods, was 22 hours long, whereas the dark period was only 16 hours long. In a 38-hour cycle perhaps a dark period of 16 hours is not inhibitory.

Another experiment employing a cycle longer than 24 hours also appears to support the importance of the light period. The schedule used was 12L—16D, and it was designed to test the simultaneous effect of a daily period of light which was known to be stimulatory (12L) and a daily period of darkness which was known to be inhibitory (16D). The experiment began in December and continued to May. The gonadal and fat responses were marked and showed some similarity to these responses under a schedule of 12L—12D (figure 11). These results, in my opinion, point to the light period as the effective period, but again the experimental design did not permit a clear-cut choice. More recent experiments employing longer dark periods, for example, 12L—20D, 16L—22D, 16L—32D, have just been concluded (May, 1958). A preliminary analysis of the gross results shows that the daily response to an effective daily photoperiod was not negated by a strongly inhibitory dark period. Hence, it seems evident that the light period is the effective part of the photoperiodic cycle. A long night is inhibitory only because it does not permit a longer or effective duration of light (photoperiod plus carry-over period).

Two additional schedules of light and darkness have been used. Although designed originally for another problem the results are pertinent here. The schedules were 16L—16D and 8L—16D—16L—8D. The first one was designed to test the inhibitory nature of a 16-hour dark period in a 32-hour cycle, the second to test whether an effective daily response could be stored when administered on alternate days. Both schedules were effective in inducing gonadal and fat responses (figure 11).

It is impossible at this time to distinguish precisely between the roles of light and darkness in the regulation of the progressive phase of the gonadal and fat responses. However, some things seem clear. 1) The total amount of darkness in a 24-hour cycle (when administered in small doses) is not the equivalent of the same amount

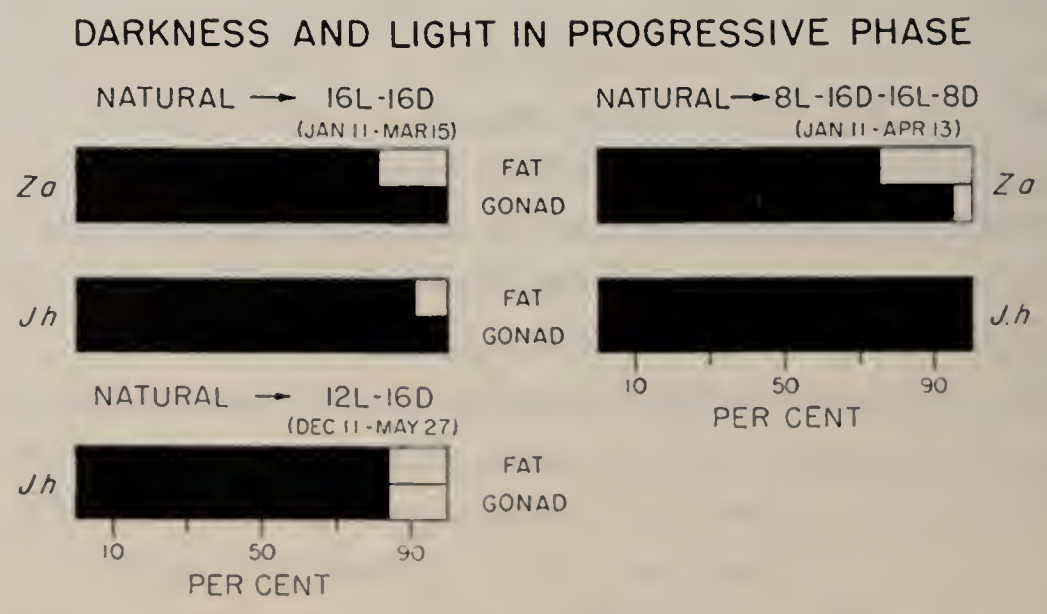

Fig. 11. Fat and gonadal responses under various schedules of light and darkness during the progressive phase. See legend for figure 9 for abbreviations.

of darkness given in a single dose. 2) Short cycles within a 24-hour period with the same proportion of light and darkness are equivalent to 24-hour cycles with regard to stimulation (5L—1D and 20L—4D), but they are not equivalent with regard to failure to stimulate or »inhibition» (1L—2D and 8L—16D) as indicated in 1). 3) With different effective schedules of light and darkness within a 24-hour cycle, there is a difference in rate and duration of response. 4) Whatever the roles of light and darkness, the daily schedule of light and darkness in nature is the critical external factor. Effective daily schedules probably result in physiological »increments of response» which are eventually manifested, or at least become more readily observable and measurable as gonadal growth, spermatogenesis, fat deposition, and increase in body weight. Figure 12 summarizes the fat and gonadal responses under all of the light-dark schedules discussed so far.

DARKNESS AND LIGHT IN PROGRESSIVE PHASE
SUMMARY OF RESPONSES

SCHEDULE	FAT	GONAD	SCHEDULE	FAT	GONAD
20L - 4D	+	+	8L - INT. N	+	+
5L - 1D	+	+	8L - 8D	+	+
1L - 2D	+	+	12L - 12D	+	+
8L - 16D	-	-	16L - 16D	+	+
(1L-.25D)^7 + 1L + 14.25D	-	-	12L - 16D	+	+
(1L-2D)^7 + 1L + 16D	+	+	8L-16D - 16L-8D	+	+

Fig. 12. Summary of fat and gonadal responses under various schedules of light and darkness during the progressive phase.

DAY LENGTH AND THE REFRACTORY PERIOD (PREPARATORY PHASE)

After a period of activity, the gonads regress spontaneously. In nature, this occurs after the breeding season, sometime in July and August for most north temperate species. During this period, long days or increasing days cannot induce gonadal activity and, hence, it has been called the refractory period. The natural termination of this period varies with the species, but it occurs usually in October or November. The refractory state can also be produced in the laboratory.

Since both the migratory and breeding cycles are closely in phase with environmental conditions, it seems unlikely that the refractory period, or the entire annual gonadal cycle, is regulated by fixed inherent rhythms of the gonads or the pituitary which operate spontaneously as some investigators have suggested (Bissonnette, 1937; Blanchard, 1941; Blanchard and Erickson, 1949; Wagner and Stresemann, 1950; Marshall, 1951).

Juncos in nature experience a reduction in day length during the summer and fall, and it was plausible that decreasing day lengths, or short days, or long nights,

could regulate the duration of the refractory period. BURGER (1947) and BISSONNETTE (unpublished data, cited by BURGER, 1947) showed that treatment with long days in the Starling eventually induced a refractory period which could only be dissipated by treatment with short days. MILLER (1948, 1951) found that treatment with long days begun in the fall in the migratory Golden-crowned Sparrow *(Zonotrichia atricapilla)* prevented the occurrence of gonadal growth at the normal time in the spring.

To determine the effect of day length on the refractory period in the junco and White-throated Sparrow, birds, whose cycles had been accelerated by exposure to 20 hours of light per day and which were in a refractory period, were treated with short days beginning in July or August. One group was exposed to 9-hours of light per day, the other to 12-hours per day. In addition, a group was retained under natural day lengths. After about 5—6 weeks of this treatment they were exposed to long days (20L—4D) beginning in August or September. The experiment terminated on October 22 for the juncos and on November 9 for the White-throated Sparrows. The juncos that were pretreated with 9-hour and 12-hour photoperiods responded, whereas the birds pretreated with natural day lengths did not (WOLFSON, 1952 b). The response in the White-throated Sparrows was similar except for a poorer response in the 12-hour group (WOLFSON, unpublished data). The responses are compared in figure 13. This experiment was repeated again in the fall during the natural refractory period and the results were generally similar (WOLFSON and SHANK, unpublished data). In still another experiment, White-throated Sparrows showed a better gonadal response when pretreated with 12-hour days for a longer period of time. In a related group of experiments, birds were exposed to 20-hour photoperiods for a maximum of 6 months beginning in the refractory period (October and early November) to test the effect of a strong stimulatory photoperiod. With few exceptions, the birds failed to respond, even at the normal time of the gonadal response

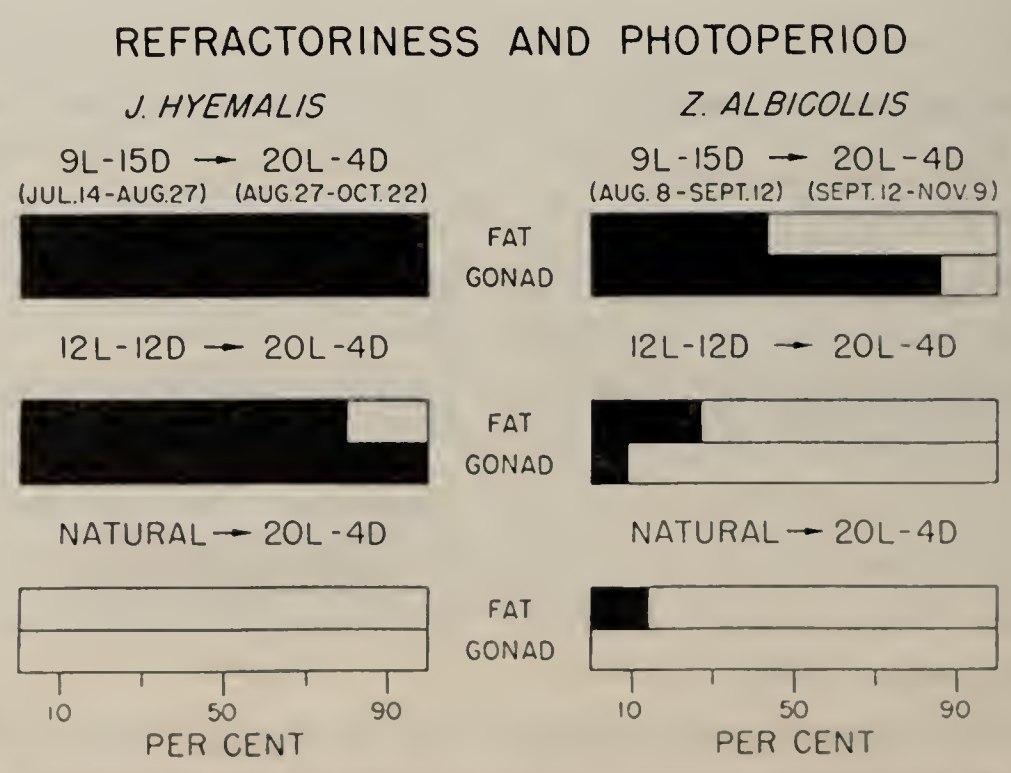

Fig. 13. Photoperiod in relation to completion of the preparatory phase.

in the spring (Wolfson, 1952 b). Similar results have been obtained in the House Sparrow by Vaugien (1954).

The results of these experiments showed that the duration of the refractory period was regulated by day length. Short days hastened its termination, whereas long days prolonged it. Whether the effective part of the photoperiodic cycle was the period of light or the period of darkness, or a relation between them, remained to be determined. However, before experiments were undertaken to determine this, another experiment was performed to test the conclusions of the above experiments.

If there is a physiological »preparation» on short days for a subsequent response to long days, then it should be possible to induce responses several times within one year, even though juncos normally show only one period of gonadal activity and two periods of fat deposition annually. Production of repeated cycles was attempted by exposing birds to alternating periods of short days (9L—15D) and long days (20L—4D) (Wolfson, 1954). The length of the periods varied, but in a total of 369 days, juncos were exposed to four periods of short days and five periods of long days, including the initial natural long days of April. Five periods of gonadal activity (including the initial active state when the experiment began), 5 periods of fat deposition, and two molts occurred within the 369 days (figure 14). Gonadal growth, fat deposition, and increase in body weight were correlated with long days. Gonadal regression, loss of fat deposits and decrease in body weight were correlated with short days. These correlations became less distinct as the experiment progressed. Prior to this study, Rowan (1929), Miyazaki (1934), Damsté (1947) and Burger (1947) had induced more than one period of gonadal activity in a year in different species of birds.

The results of this experiment confirmed the conclusion of the previous series on the refractory period, that short days in the fall regulate a reaction which enables the bird to respond to subsequent photoperiodic treatment. Without this »preparatory period» the bird does not respond. Although the bird is »refractory» to long days in the fall, it is undergoing a reaction which is regulated by day length (short days) and which is necessary for a subsequent response. Hence, it seems more appropriate to call it the preparatory period or phase. This period is then followed by the progressive phase of the cycle.

Role of light and darkness in the regulation of the refractory period (preparatory phase)

Having established the requirement for short days during the preparatory period, the next problem was the determination of the effective part of the short days. Was it the short photoperiods or the long dark periods? A variety of schedules was used during the natural refractory period which was followed by subsequent treatment with long days (20L—4D) beginning in December or January. The schedules used

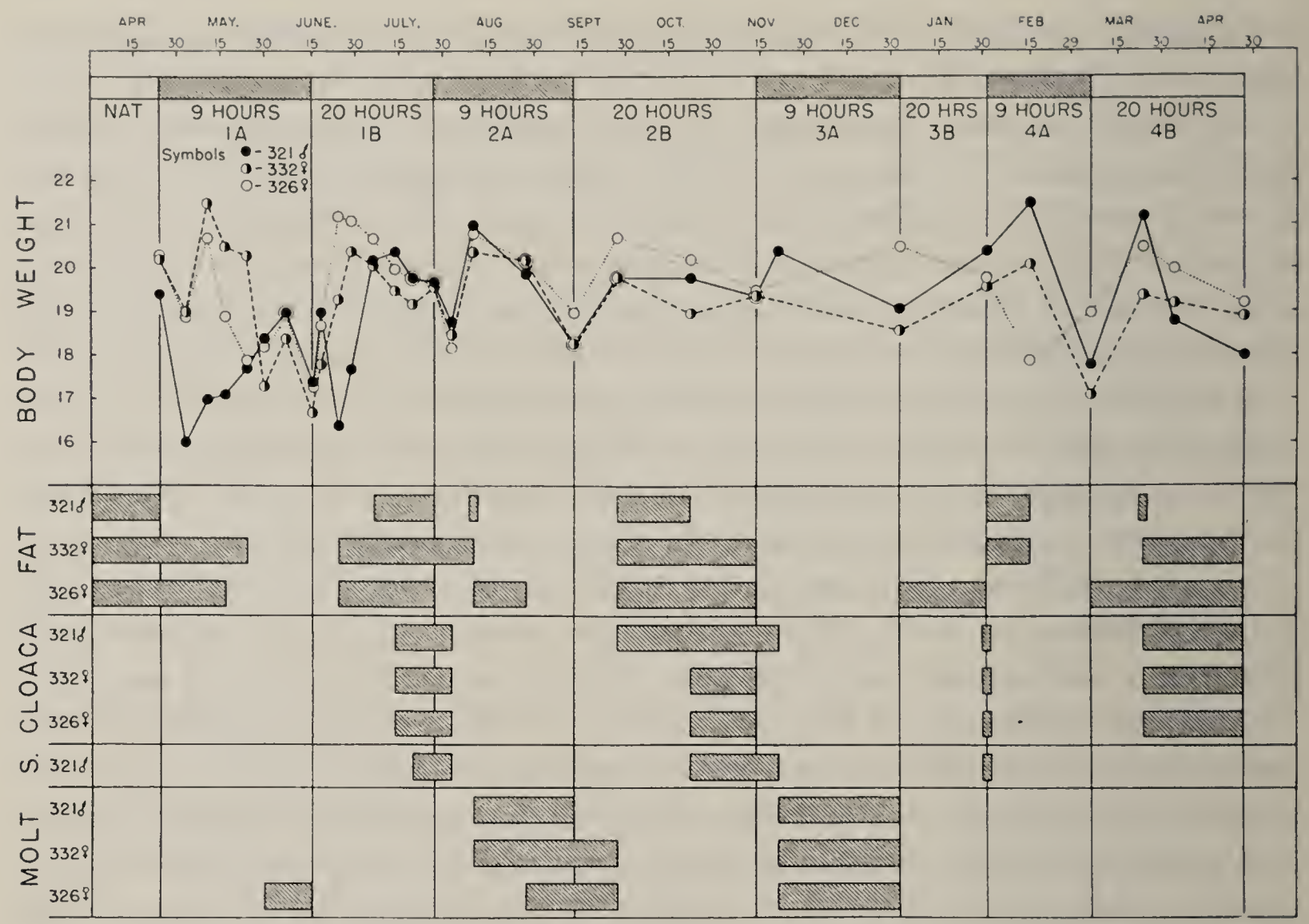

Fig. 14. Responses in juncos for the duration of the experiment. Body weight is given in gms. The horizontal bars in the lower half of the figure indicate the duration of the response from the first until the last time it was observed. Where only a few observations were made in some periods, the duration bar represents only the occurrence of the response (as for example, for the cloaca and sperm at the end of period 3 B). Molt response indicates a molt comparable to the annual molt. The abbreviation S. refers to occurrence of sperm, which were obtained by applying pressure to the »seminal vesicles» (WOLFSON, 1952 c).

and their effectiveness in inducing the preparatory phase are given in figures 15—18 and summarized in figure 19.

The results of the first experiments demonstrated that it was not a short period of light per se, nor the total amount of separate doses of light and darkness in a given day, nor the proportion of light to darkness in a short cycle that was effective. Rather, it was a single period of darkness, 12 hours long, or longer, in a 24-hour cycle that was the effective part of a short day (figures 15, 16, 17). A 16-hour dark period was generally more effective than a 12-hour period, which seems to be near the threshold for the minimum effective duration of the dark period.

The next question was whether a 16-hour dark period per se was the effective stimulus, or whether a long single dose of light was inhibitory. To answer this, birds were exposed to schedules of 16L—16D and $(1L—2D)^7—1L—16D$ during the preparatory period and then treated with long days (20L—4D). Both schedules were ineffective and corresponded to long days (figure 18). That they were actually long days was established by the response of birds to those same schedules during the

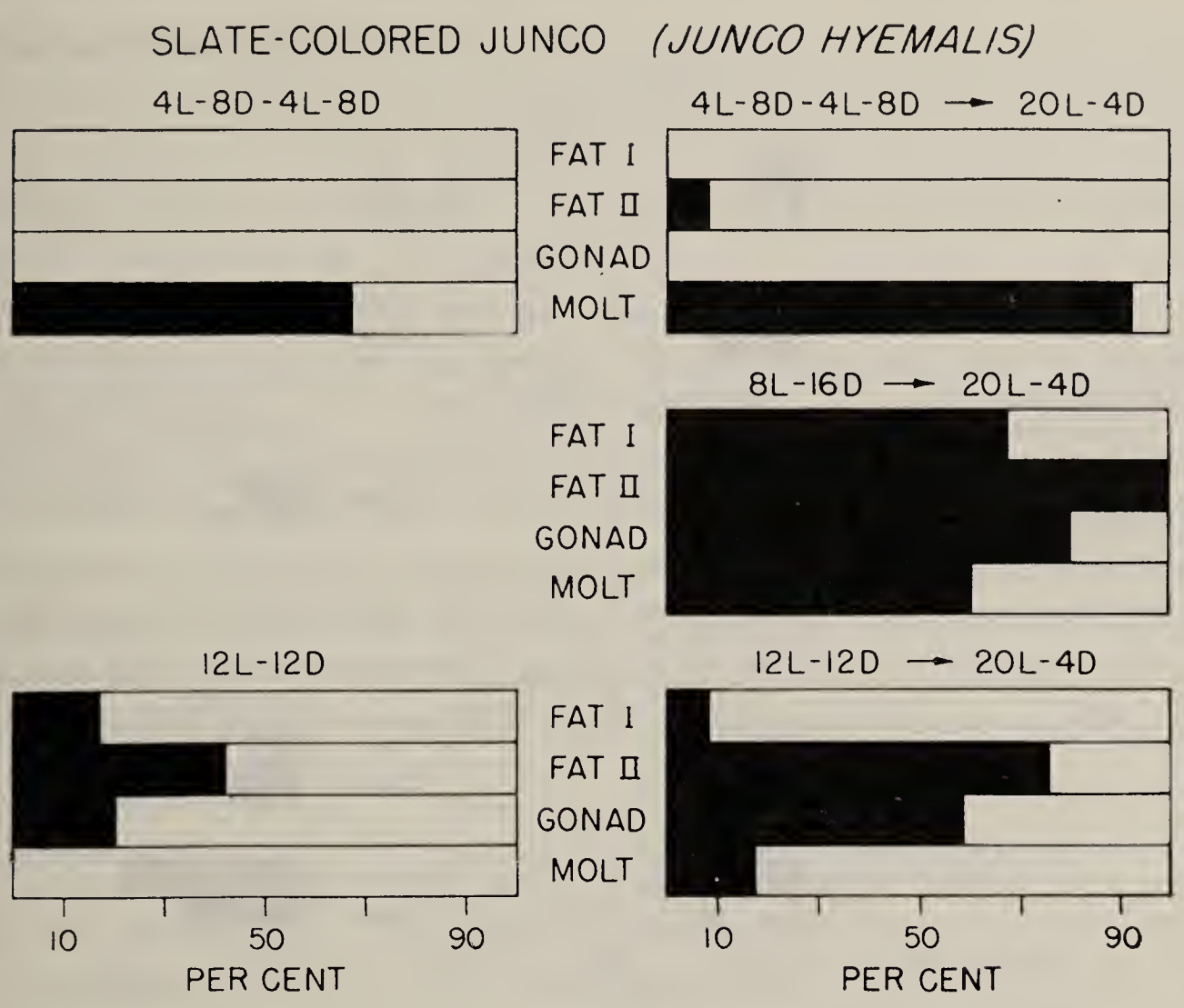

Fig. 15. Effectiveness of various schedules of light and darkness in inducing completion of the preparatory phase in the Slate-colored Junco. Fat I denotes the response in the fall, fat II response in the winter after transfer to long days. Molt refers to the annual molt.

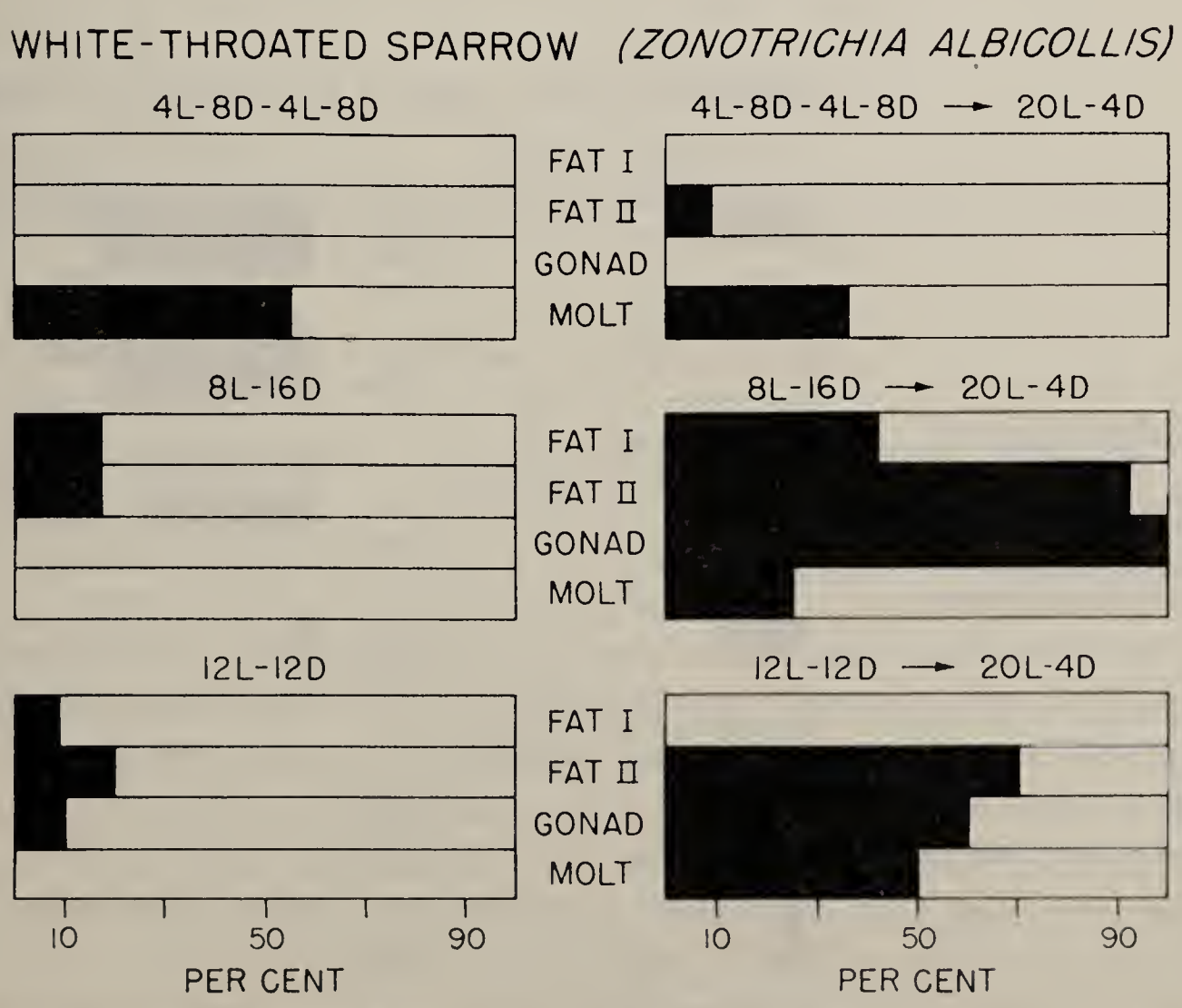

Fig. 16. Effectiveness of various schedules of light and darkness in inducing completion of the preparatory phase in the White-throated Sparrow. See legend for figure 15.

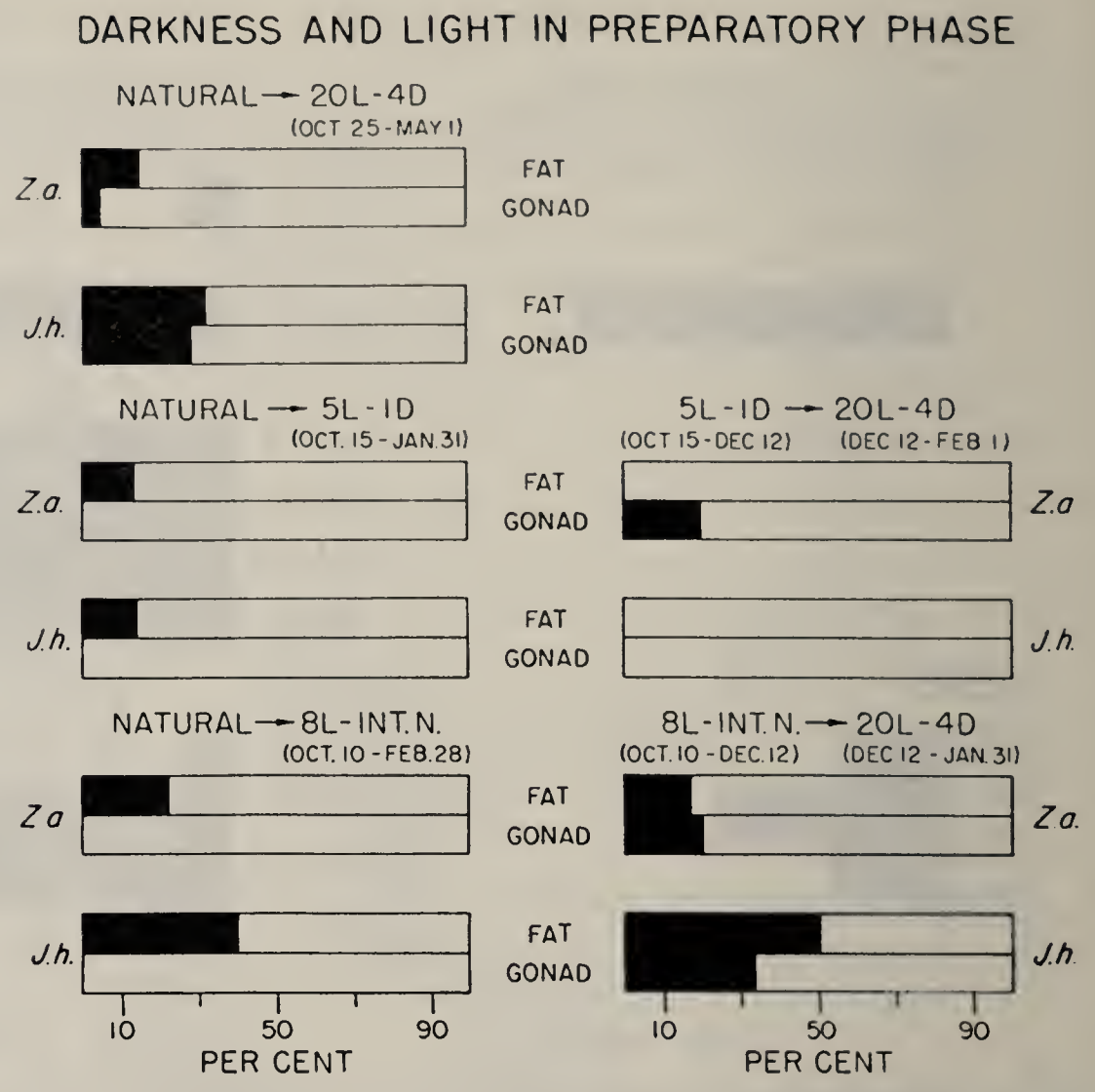

Fig. 17. Effectiveness of various schedules of light and darkness in inducing completion of the preparatory phase. Abbreviations as in figure 9.

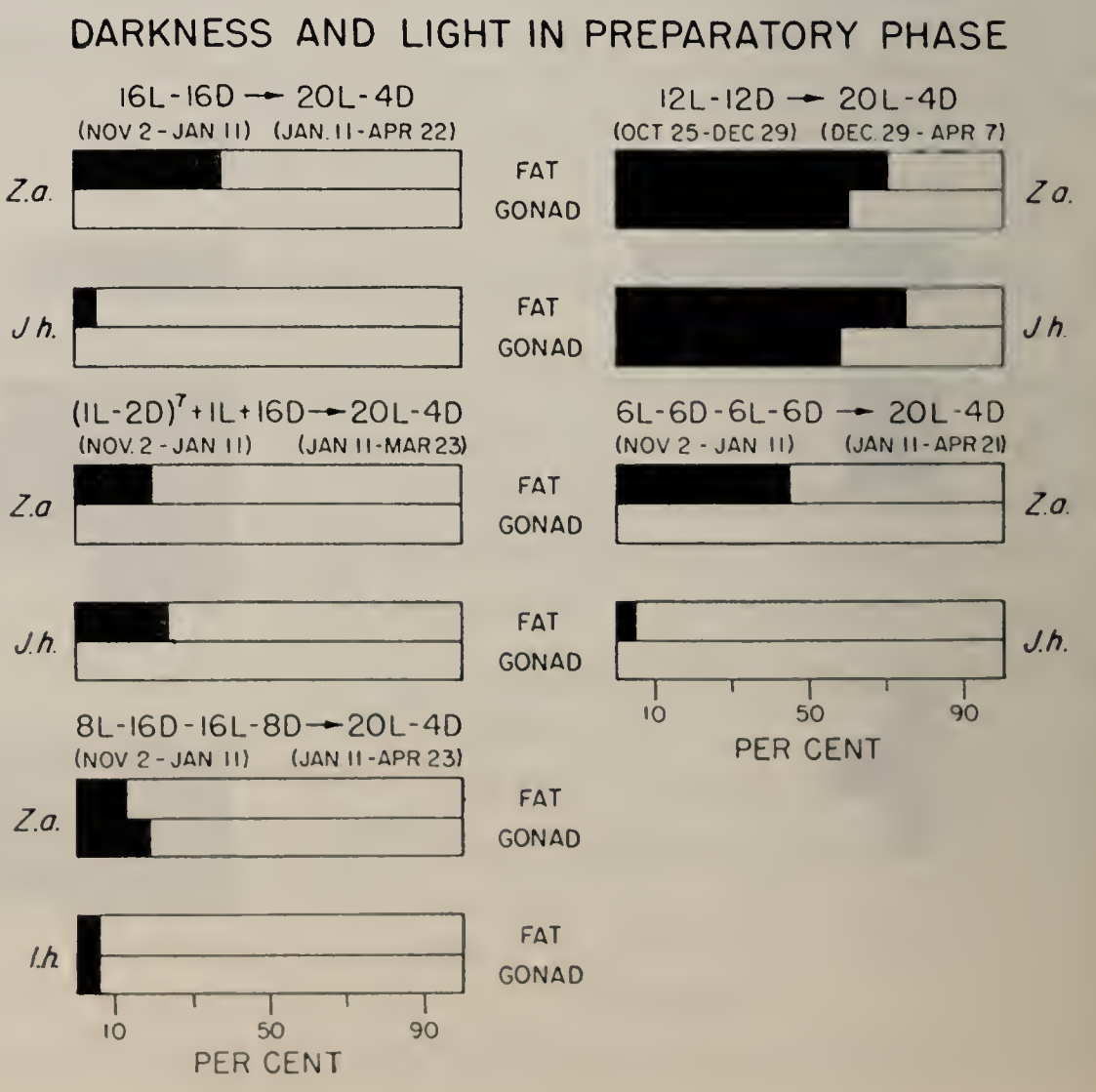

Fig. 18. Effectiveness of various schedules of light and darkness in inducing completion of the preparatory phase. Abbreviations as in figure 9.

winter as described earlier. The results indicated that a 16-hour dark period per se is not the effective stimulus. There is some relation apparently between the duration of the light period and the duration of the dark period, or there is a single dose of light which is inhibitory irrespective of the length of the dark period. Further studies are needed to explore these alternatives.

Another question of interest was whether a bird can »store» each daily increment of response during the preparatory phase. The schedule used was the same as that in the progressive phase —8L—16D—16L—8D. It turned out to be a long day during the preparatory period just as it was during the subsequent progressive period (figure 18). This may have been due to the fact that the bird was reacting to the schedule not on a daily basis, but rather as 8D—8L and 16D—16L, both of which are known to act like long days. To answer the question of whether the bird can store a daily stimulus until a threshold is reached, or whether continuous daily effective photoperiodic schedules are required, further experimentation is needed.

DARKNESS AND LIGHT IN PREPARATORY PHASE
SUMMARY OF RESPONSES

SCHEDULE	FAT	GONAD	SCHEDULE	FAT	GONAD
9L - 15D	+	+	20L - 4D	-	-
8L - 16D	+	+	5L - 1D	-	-
4L - 8D	-	-	8L - INT. N.	-	-
12L - 12D	+	+	$(1L - 2D)^7 + 1L + 16D$	-	-
6L - 6D	-	-	16L - 16D	-	-
			8L - 16D - 16L - 8D	-	-

Fig. 19. Summary of effectiveness of various schedules of light and darkness in inducing completion of preparatory phase.

DISCUSSION AND SUMMARIES

When the results of all of the experiments which have been described so far are considered in relation to migratory behavior and reproductive rhythmicity, it is evident that day length in nature plays an important regulatory role in a number of ways. I shall consider migration and reproduction separately, since the data and the interpretations, although similar, are not identical for both. It is not clear yet whether the development of the premigratory physiological state is dependent on the activity of the gonads, but in nature gonadal recrudescence is correlated with the onset of migration. In view of our ignorance of the precise roles of light and darkness, I shall discuss and summarize the regulation of migration and reproduction first in terms of day length, with particular reference to what goes on in nature, and then consider the roles of light and darkness. Finally, I shall discuss briefly the question of an inherent rhythm of the endocrine glands, the problem of day length

in relation to the timing of spring migration in equatorial and transequatorial migrants and day length and breeding cycles in the tropics. A more extensive discussion is presented in another paper (Wolfson, 1959a). Brief reviews of the neuroendocrine mechanisms involved have been presented by Farner (1959) and Wolfson (1959b).

Day length and migration. The data available demonstrate that two phases or periods are involved in the timing of spring migration. The first occurs in the late summer and fall and is called the preparatory phase; the second begins in late fall and continues through the winter until the time of migration in the spring and is termed the progressive phase. The preparatory phase is prerequisite to the progressive phase.

The preparatory phase in nature is apparently regulated by the shorter day lengths of the fall. In the laboratory, this phase was induced at different seasons of the year by subjecting birds to short days (9L—15D). Twelve hours of light per day appears to be near the threshold for the maximum day length which can act like a short day. Long days (16L—8D) inhibit the occurrence of the preparatory phase and the appearance of the subsequent progressive phase. Therefore, the short days of fall are actually regulating the time of occurrence of the migratory behavior and breeding cycle which appear six to seven months later. The time required for the completion of the preparatory phase is six weeks or less. Whether the duration of the preparatory phase is related to the length of the short day has not been determined, but a few relevant data suggest that there may be some relation between the length of the dark period, the duration of treatment, and the rate at which the preparatory phase proceeds.

After the preparatory phase has been completed, the progressive phase begins. In nature, it probably begins automatically in late November and December when the days are short, but *the rate at which it proceeds* is governed by day length. The spring premigratory physiological state was induced by means of long days about 80 days ahead of its natural occurrence in a majority of the birds. With a short day (9L—15D) the same state appeared in about 160 days, which was 40 days later than its occurrence in nature. Approximately the maximum rate of response occurred with a day length as short as 15.5 hours, the minimum rate with a day length of 9 hours, but shorter day lengths were not tried. Nine hours was used as the minimum, because this is about the shortest day to which juncos are exposed in nature at Evanston (excluding civil twilight).

It is important to emphasize here that the progressive phase proceeded *when there was no increase in day length.* When the birds were exposed to 9-hour photoperiods beginning December 4, they had already completed the preparatory phase under natural day lengths. On December 4 their day length was reduced from approximately 10 hours under natural conditions (including civil twilight) to 9 hours, and it remained constant at 9 hours thereafter. Yet, these birds achieved the spring premigratory physiological state, on the basis of their fat deposition and body weight,

but about 40 days later than usual. Their reproductive organs were, however, somewhat below the normal. About 60 % of the birds released in June after being held on 9-hour days since December undertook a migration.

In view of our earlier knowledge which showed the stimulatory effect of increasing day lengths during the winter, it must be emphasized that gradually increasing day lengths (or an increase in day length) are not necessary to induce spring migration. The role of day length, once the birds are ready to respond, is the regulation of the rate at which the response proceeds. The progressive phase proceeds spontaneously without increases in day length and when the days are as short as the shortest days in December and remain short. This is a major change from the conclusions of the earlier experiments in which migration was induced out of season by subjecting birds to artificial increases in day length (Rowan, 1929; Wolfson, 1942, 1945).

After the birds are in the premigratory physiological state, the length of time they remain in this state is a function of day length. Long days dissipate the state more quickly than short days, and under short days (12L—12D and 9L—15D) the birds may not lose their fat. A change from long days to short days will also dissipate the state rapidly.

In nature, the spring premigratory physiological state ends when the birds arrive on their breeding grounds, or shortly afterward. After the breeding season, the gonads regress, the birds molt, and, subsequently, there is a physiological change, which precedes the onset of fall migration. Nothing is known about the factors which regulate this state. When the fall migration gets underway in September and October the day lengths have reached a length which is effective for the beginning of the preparatory phase of the next spring migration. And thus, a new cycle begins.

Role of light and darkness in the migratory cycle. The available data suggest that in the preparatory phase, the effective part of the short days is the dark period. It seems likely that there is dark-dependent response which requires a daily uninterrupted dark period of at least 12 hours duration. This response cannot occur when a greater total amount of darkness is given per 24 hours in smaller doses, for example 4L—8D—4L—8D. Or, if the dark-dependent reaction goes on during short dark periods, it cannot summate to give an effective daily response or a response after the lapse of many days. The absence of an inhibitory reaction produced by long days is apparently not a factor, since with short periods of light, the same small total amount of light per day, and the same ratio of light to darkness the preparatory phase did not occur (for example, 4L—8D—4L—8D was negative, whereas 8L—16D was positive; 6L—6D—6L—6D was negative, whereas 12L—12D was positive). However, more studies are needed to establish this point, because of the possibility of carry-over effects of the light periods. The responses induced by each daily effective period of darkness either summate to a threshold or dissipate the »refractoriness» gradually. Eventually, the bird completes the preparatory phase and is prepared to begin the progressive phase.

Although the present data favor the interpretation that the uninterrupted period of darkness is the effective stimulus of the short day, the results of the 16L—16D experiment indicate that this interpretation must be accepted tentatively. If a 16-hour dark period in a 24-hour cycle is the effective part of a short day, why doesn't the preparatory phase occur under a schedule of 16L—16D? Obviously, a 16-hour dark period *per se* is not the only factor governing the reaction in the preparatory phase. A long light period can negate the positive effect of a long dark period. The ratio does not seem to be an important factor, since 12L—12D gives a positive effect. Here again, the problem of carry-over effects of the photoperiods may be involved, nevertheless it is clear that the data show some effect of the photoperiod. Thus, although the evidence points to the dark period as the critical factor in a short day, there also seems to be some relation between the photoperiod and the dark period, the net effect of which may be positive or negative, depending on the length of the photoperiod.

One final and significant observation must be noted, which bears on the previous statement that the progressive phase proceeds spontaneously once the preparatory phase has been completed. A schedule of 12L—12D is uniformly effective in the preparatory phase in late July and August in the junco. Yet, when birds were treated with this schedule beginning in October and were retained under the same conditions until May, well past the natural occurrence of the premigratory physiological state, or were treated with 20 hour photoperiods beginning in December, many failed to respond. Birds held under natural day lengths during fall and then treated with a schedule of 12L—12D beginning in December responded well. If 12L—12D is an effective schedule for preparation in late summer and is also an effective schedule for the progressive phase, why didn't the birds treated with 12L—12D beginning in October respond uniformly? To determine whether the birds held until May had undergone the preparatory phase, a few remaining birds were treated with 20-hour photoperiods beginning in late May. They responded well, and hence, had completed the preparatory phase. The failure in these birds was apparently in the progressive phase. There was also failure in the preparatory phase, since some birds which were exposed to 20-hour photoperiods beginning in late December, also failed to respond. The differences in »preparation» and »responsiveness» between the birds treated in summer and fall may stem from the differences in the history of the birds before the experiments. Whatever the explanation, what is significant is the observation that in some birds exposure to a schedule of 12L—12D in the fall modified the usual response to 12L—12D days begun in December. It should be noted here also that birds exposed to continuous light responded well and as rapidly as birds exposed to schedules of 20L—4D and 15.5L—8.5D. Whatever the effective stimulus is, the *daily* responses ultimately induce the migratory response.

An interesting difference between the »light and dark» reactions of the preparatory and the progressive phases is that in the preparatory phase, where the dark period seems to be the critical factor, the effects of shorter dark periods in a 24-hour cycle

do not summate to give an effective daily stimulus. In the progressive phase, where the light appears to be the critical factor, the effects of short light periods do summate to give an effective daily stimulus when there is no inhibitory duration of darkness in a 24-hour cycle. In the preparatory phase a long light period *per day* appears to be inhibitory, whereas in the progressive phase, a long dark period *per day* appears to be inhibitory. In both phases, the data show clearly that the 24-hour cycle is highly significant. It is possible that an inherent 24-hour rhythm or other innate rhythms in the bird are related to the migratory and reproductive responses to photoperiodic schedules and that must be explored in future studies.

Day length and reproduction. The regulation of the reproductive cycle in the male also occurs in two phases, the preparatory and the progressive. The preparatory phase occurs in late summer and fall, the progressive phase in late fall, winter, and spring. As with migration, the preparatory phase is prerequisite to the progressive phase.

The regulation of the preparatory phase by day length is the same as that for migration. There are some differences, however, in the responsive phase. A 9-hour photoperiod per day induced migration at a slow rate. However, only one junco showed a good testicular response (complete spermatogenesis, but not maximum size) under a 9L—15D schedule and that was almost twelve months after the experiment began (December 4 to November 23). The other birds which were sacrificed during the course of the experiment, showed only a slight development. Hence, a short photoperiod is much more retarding in the progressive phase of the reproductive cycle.

Once the preparatory phase has been completed, the progressive phase is probably initiated spontaneously and proceeds at a rate which is determined by the day length. Complete spermatogenesis (Stage 5 of Wolfson) was first achieved in 37—38 days under the longest days, 24L and 20L—4D; in about 78 days with a schedule of 15.5L—8.5D; in about 150 days with a 12L—12D schedule; and in about 166 days under natural day lengths.

The duration of maximal reproductive activity is also regulated by day length. The shortest durations were produced by long days, the longest by days with 12-hour photoperiods. With a schedule of 12L—12D begun in April, a few birds maintained reproductive activity for 3 to 6 times as long as the normal duration of about two months; when begun on December 4, no gonadal regression was observed in one experiment.

Regression of reproductive activity occurs spontaneously in nature, and the time that it begins is obviously under the control of day length. It can also be induced experimentally by short days. After regression the birds enter the preparatory phase, and a new cycle is ready to begin. The long days of late summer probably initiate and maintain the refractoriness or prevent its rapid dissipation. It seems worthwile to keep in mind a possible distinction between gonadal regression, which may be an innate feature of the reproductive cycle, and refractoriness which may be a feature induced by the long days of the temperate latitudes.

Role of light and darkness in the reproductive cycle. The conclusions and discussion given above in relation to the migratory cycle are applicable here.

Inherent rhythm and migratory and reproductive periodicity. Ever since the discovery that day length influences the reproductive and migratory cycles, there have been suggestions that these cycles, in whole or in part, are regulated by internal rhythms which are independent of external factors such as day length. Among current investigators, BLANCHARD (1941) and MARSHALL (1951, 1955) emphasize the role of an internal rhythm. The studies reported here and the recent work of BURGER (1953), FARNER and WILSON (1957), and MILLER (1954 b, 1955) demonstrate the regulation of the entire annual cycle by day length. Moreover, day length does not act like a trigger that sets off an inherent cycle with an innate periodicity and amplitude. Every phase of the reproductive and migratory cycles has been shown to be influenced by day length — the time of occurrence, the rate of development, the extent of development, and the duration of the preparatory and progressive phases. Only one process appears to be inherent and that is the initiation and occurrence of regression of the testes after a period of reproductive activity. But even this is open to question since no regression was observed in a 12L—12D experiment begun in December and continued for a year. The time of regression and the extent of regression can be manipulated by day length. More studies are needed to determine whether the process of regression and the re-organization of the testis are independent of environmental factors (MARSHALL, 1951).

Another possible inherent aspect of the cycle is the initiation of the progressive phase. After birds have completed the preparatory phase, the migratory response and spermatogenesis usually begin spontaneously. But they do not occur until after the completion of the preparatory phase.

If the initiation and occurrence of regression and the initiation of the progressive phase are inherent processes and independent of external factors, then their periodic occurrence may be rightly called an inherent rhythm. The term rhythm, however, would apply only to the *alternation of these processes* and could not be construed as implying the time of occurrence, rate of development, amplitude, or duration of the various phases in the cycle, all of which have been clearly shown to be influenced by day length. Further studies are needed which will permit precise definition of the physiological responses during the photoperiods and the dark periods before we will be able to distinguish between inherent and independent reactions and reactions induced and regulated by environmental factors. Admittedly, the present interpretations which are based only on the manifest responses are not satisfactory.

Day length and the timing of spring migration in equatorial and transequatorial migrants. On the basis of the experimental results and the interpretations presented here, the timing of spring migratory behavior in migrants wintering on the equator, in the tropics, or in the southern hemisphere can be explained. Experimental work must be done of course with equatorial and transequatorial migrants to test the hypothesis presented, but the data available so far for north temperate species sup-

port it. The relatively constant day lengths of the equatorial region can no longer be regarded *a priori* as non-regulatory. Constant photoperiods of 12 hours have been shown to be effective and the duration of the photoperiod, moreover, regulates the rate of response. Hence, birds wintering in the equatorial region could be responding to the relatively constant day lengths of 12 hours. The birds that cross the equator and winter in the subtropics or temperate regions of the southern hemisphere are exposed to gradually increasing day lengths after they arrive in late October or November and to gradually decreasing day lengths after December 21, which reach a length of about 12 hours on March 21. Therefore, they are exposed during their entire stay on the wintering grounds to long days which, although they increase gradually to a maximum and then decrease gradually to 12 hours, would remain at an effective photoperiodic level, judging from our experimental work with juncos.

The main problem in equatorial and transequatorial migrants, as I see it, is not the effect of the day lengths on the wintering grounds, but the relation between day length and the preparatory phase and the initiation of the progressive phase. At the outset, it seems highly likely that there is a preparatory phase in these birds that is regulated by day length rather than being a self-regulated spontaneously expressed rhythm. Unlike the junco, these migrants would not experience days shorter than about 12—13 hours, or nights longer than about 11—12 hours. Is this a short enough day or a long enough night to complete a preparatory phase? Since some juncos could »prepare» on a constant 12L—12D schedule, it is probable that these migrants could also prepare under the photoperiodic conditions they would experience from September to November while migrating from their north temperate breeding grounds to their wintering grounds. Since only 6 weeks of treatment with 12L—12D in July and August was enough to complete the preparatory phase in the junco, it is highly probable that equatorial and transequatorial migrants would be exposed to a sufficient number of 12—13 hour days during the period of fall migration to complete their preparatory phase, or at least to reach the point where slightly longer days would not prevent, but perhaps would delay, completion of the preparatory phase. An alternative explanation is that the effective day lengths during the preparatory phase are longer than those in the junco. Species differences in the relation between day length and the preparatory and progressive phases are to be expected. It is interesting to note that in nature juncos winter where they will experience dark periods longer than 12 hours, hence, spontaneous initiation and rapid development of the progressive phase is assured. The regulation of the preparatory phase and of the initiation of the progressive phase is the critical problem in the regulation of spring migration in equatorial and transequatorial migrants. Experimental studies with equatorial and transequatorial migrants are currently underway in our laboratory to test the hypothesis presented.

Day length and breeding cycles in the tropics. Studies of breeding cycles at all latitudes led Baker (1938) to the conclusion that »The main proximate causes of the breeding seasons of birds in nature are thought to be temperature and the length

of day in the boreal and temperate zones, and rain and/or intensity of insolation near the equator.» Recently, a reexamination of the problem led to the same general conclusion that day length and temperature in the higher latitudes and humidity and rainfall in the tropics are correlated with the breeding seasons (THOMSON, 1950; MOREAU, 1950; LACK, 1950 a, 1950 b; VOOUS, 1950; SKUTCH, 1950). The significance of these climatic factors is believed to lie in their effect on food supply. Breeding seasons are regarded as an adaptation and occur apparently when the young can be reared at the time of maximum food supply. If the breeding season is adapted to environmental conditions operating toward its close, other factors must be postulated for the initiation of the cycle. Although day length and temperature are acceptable for higher latitudes, in the tropics both »are too nearly constant to offer a possible explanation» (THOMSON, 1950, p. 182). There is little doubt that the early experimental studies which employed increasing and decreasing day length to alter the gonadal cycle and the fact that day length and temperature vary periodically in higher latitudes have played a large part in the derivation of the above conclusions. The new experimental findings presented above, however, suggest that we should proceed cautiously before ruling out day length as a regulatory factor in the tropics simply because it is relatively constant. It has been shown that some tropical species respond to day length and the gonadal responses of the juncos treated with a 12L—12D schedule simulated some aspects of the gonadal cycle in tropical species. During the last few years additional studies have been made of breeding cycles in the tropics, a few experiments have been performed, and the effect of external factors, particularly drought and rainfall, on reproduction have been studied (MILLER, 1954 a; KEAST and MARSHALL, 1954; MARSHALL and DISNEY, 1956; MARSHALL and DISNEY, 1957; SERVENTY and MARSHALL, 1957). (See WOLFSON 1952 a and 1959 a for discussion and review.)

In summary, the relation between day length and the gonadal cycle in tropical species is not known, but the point that must be emphasized is that day length cannot be ruled out *a priori* as a fundamental regulator of migration and breeding cycles in the tropics simply because it is relatively constant. In a similar vein, day length should not be ruled out at other latitudes, because not all birds are breeding when the days are increasing, or because the gonads begin their growth phase when the day lengths are decreasing or relatively constant. When day length is suggested as a regulatory factor at all latitudes it is not meant to imply that all birds will react to it in precisely the same manner. On the basis of the findings presented in this paper, it is clear that the day length conditions in the tropics could regulate the gonadal cycles in a variety of ways, and it is not reasonable to think of light only in relation to the progressive phase. Our experiments indicate that day length not only regulates the time of initiation of the progressive phase of the testis, but also the rate and amplitude of the progressive phase, the duration of maximum activity, the time of initiation, rate, and extent of regression, and the duration of the preparatory phase. There is no reason to believe that all of these aspects will be regulated

by day length in precisely the same manner in all species. Nor must all of these aspects be regulated by day length. Regulation of a few is all that is needed for day length to be a primary factor in the timing of breeding seasons. It should be recalled that races of the same north temperate species responded differently to identical experimental conditions of day length. When tropical species have been studied experimentally as intensively as north temperate species, they will surely show differences in their response to light and dark periods. Moreover, other environmental factors, such as rainfall, diet, and psychic factors may prove to be important modifying factors with different degrees of effectiveness in the preparatory, progressive, and regressive phases. Only day length has been shown so far to be a primary regulatory factor, and its relation to gametogenesis and reproductive rhythmicity in tropical species remains to be determined by extensive experimental studies.

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The Overfishing Principle Applied to Natural Populations and their Food-Resources: and a Theory of Natural Conservation

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1. OVERFISHING

In exploiting the living resources of the sea man is still essentially a hunter, obtaining by his skill and enterprise a catch which is a primitive product of nature. Anything corresponding to the methods of cultivation, used by the farmer to increase the yield of food from the land, can be practised in the sea only on a negligible scale. Thus as far as the fisheries are concerned, man can be regarded as an ordinary predator exploiting a natural prey for food.

Events of recent history have shown beyond doubt that fishery resources are not inexhaustible. One of the clearest demonstrations has come from the whale-fisheries of the North Atlantic area, which depended for some 350 years principally on the Bowhead or Greenland Right Whale *(Balaena mysticetus)*. From about 1500 onwards the waters of Newfoundland and the Gulf of St. Lawrence, of Spitzbergen, East Greenland and Davis Strait have been successively fished out. Towards the end of the 18th century the effort expended and the annual catch were both still growing, and yielding very profitable returns, especially in Davis Strait; but by 1830 the peak of production had already been passed, and the northern Right-whale fishery had entered upon a swift decline. Scarcely forty years later, in 1868, the year's catch by the Scottish fleet of thirty ships amounted only to 208 Right Whales — an average of seven apiece. For still another 50 years, following the introduction of steam vessels and the harpoon gun, the faster-moving Blue and Fin Whales *(Balaenoptera* spp.) were pursued, and the declining fishery was thereby sustained; but before 1914 the focus of the whaler's attention had already shifted to the Antarctic. The Right Whales, though protected, have never recovered in numbers; and in the British seaports, such as Peterhead, Dundee, Whitby and Hull, which once grew rich on whaling, the industry and all who took part in it are extinct (cf. Jenkings, 1921).

A similar history has followed the intensive pursuit of the true fishes, such as Cod, Haddock, Plaice and Halibut. The North Sea has proved unequal to the demands

made upon it by the countries of western Europe, and in the last fifty years the supply of fish has been maintained only by sending vessels ever further afield. The 1914—18 war put a temporary halt to the exploitation of the most heavily depleted fishing grounds in home waters, and immediately after the war the stocks of Plaice, Haddock and Cod were found to have made spectacular recoveries. (The same happened again in 1946.) The size of individual fish caught, the catch per unit effort and the total yield were all notably greater; but the effect was quite short-lived, and under renewed pressure the stocks soon fell below what they had been in 1914 (cf. RUSSELL, 1942).

This episode first drew attention in a convincing manner to the reality of overfishing. Expositions of the general underlying theory were given by BARANOV in 1918 and by RUSSELL in 1931, and since that time the problems of productivity and management have increasingly commanded the attention of fishery research-workers in all parts of the world. The recent publication of BEVERTON & HOLT's (1957) penetrating analysis of the dynamics of exploited fish-populations marks the latest advance in our understanding of the subject.

The position can be represented simply in the following way. The yield from a virgin fishery may safely be increased, by a sufficient concentration of effort, until it reaches a certain optimum level, which is the highest level of cropping that the stock can sustain continuously without being depleted. In the long run this is the yield which gives the greatest possible returns. However, when a free commercial fishery reaches this particular point in its development it is generally proving highly profitable, and goes on attracting additional capital and effort. Increased effort for the time being increases the total yield, and this may induce the intensity of exploitation to rise still further. In spite of the fact that the optimum is being exceeded, the catch per unit effort does not necessarily fall appreciably at first, and even when it does so the margin of profit may remain sufficient for some considerable time to compensate for the outlay of effort. Thus by the time the fishery ceases to be profitable and there is consequently a relaxation of fishing intensity, the stock will have become to a greater or less extent depleted. Even though the fishery is not completely exhausted, economic pressure will tend to prevent it recovering and to keep it at the level of marginal profitability, and the food value annually yielded will continue to be less (usually much less) than it could and would be under ideally efficient management. Under a free system of fishing the greater the potential profitability of the fishery, the severer will be the degree of overfishing, and the larger will continue to be the deficit between actual and potential yields.

This situation may be improved and in theory completely overcome by reaching a mutual agreement or convention to limit the effort, so as to permit the stock to build up, regain, and preserve its level of maximum productivity. In practice this is not easy either to achieve or operate; even with the southern whale-fishery, which is nowadays very strictly controlled by the International Whaling Commission, the stock of Blue Whales has suffered disquieting diminution over the past ten years.

An equally difficult problem of quite another kind is to determine the critical size of effort required to yield the optimum catch. It can be discovered only by the careful collection and rigorous analysis of all the relevant statistics. There is no »red light» which indicates when the optimum is being exceeded, and indeed this generally happens, as has been pointed out, quite unperceived at the very time that the fishery is experiencing its greatest boom. Any downward trend is effectively masked at first by the wide natural variations in productivity which are to be expected from year to year; and thus the pinch is felt, and the true situation revealed beyond doubt, only a long time after the event, by which time the damage is already severe.

For the purposes of the present paper there are two all-important conclusions to be drawn from this analysis: first, that overfishing can be prevented only by accepting or imposing a man-made convention; and second, that the optimum level of exploitation, which gives the biggest possible sustained yield, can be determined only by long-term experiment.

This situation is now very fully understood. What appears not to have been considered hitherto is the fact that, with rather rare exceptions, a situation which is fundamentally identical faces every natural population of animals in exploiting its food-resources.

For the moment we may confine our attention to predators and their prey, though it will be shown afterwards that the situation is no different for herbivores. The ultimate population-density of the predator depends on that of its prey, and it can remain at its highest level *only if the prey is subjected to the optimum catch and not overfished*. In the nature of things this means that an efficient predator population must frequently accept a limitation of effort in the midst of abundance, in order that a similar productivity may be conserved and assured for the future. For example, it may be safe to take on the average up to 25 per cent of a particular prey per annum, though a 50 per cent toll would lead to depletion and rapidly diminishing returns; in some manner the predators' effort must therefore be limited to taking no more than the optimum amount, even though at the time the prey continues to be relatively abundant and easy to catch. If, indeed, the predators were to exercise a completely free and unreserved pressure on their prey, »overfishing» would be as certain and invitable a consequence as it is in unchecked human predation on food-fishes.

2. A THEORY OF NATURAL CONSERVATION

It is possible to put forward a general theory to explain how overfishing is prevented in animal populations. The truth of it cannot be fully demonstrated in the space of a few pages, though it may very readily be seen to accord in quite a striking manner with the known facts. The theory is that, instead of competing directly for food in a free-for-all scramble, individuals in a population compete instead for a purely conventional substitute, which is in effect the *right* to take food.

Among all the higher animals such as birds competition for this right assumes two apparently distinct forms, though in the end they turn out to be different only in the degree of symbolism they involve: the first form is identifiable as a contest for the occupation and use of real property; and the second as a contest for a sufficient status in the social hierarchy or peck-order. Success in either or more usually both of these forms of competition confers the right to the uncontested use of every resource, including food. It may be added in parenthesis, since it does not concern us here, that success of exactly the same kind is equally entailed in securing the right or qualification to start breeding. Each of these objects of competition must be examined a little more closely.

The simplest form of occupation of real property is the use of a comprehensive territory, which supplies the occupier with all the necessities of life and from which other individuals are excluded. Provided the territories are sufficiently large, the population-density will be prevented from rising above the optimum level, while each territory-holder enjoys ample resources for his needs and is in no danger of overfishing. This is exactly what appears to happen in many species of birds, especially in the breeding season. It should be noted that the limitation of population-density imposed by a territorial system depends on purely artificial and self-imposed convention, being due to an adaptation of the behaviour of the participants, perfected by natural selection.

There are many alternative systems of property-tenure all more complex than this: for example an individual may become a member of a social group, by virtue of having successfully won a nest-site in a colony (or a sleeping-place in a roost), and this may give a free right to the use of communal food-resources within a communal territory, as well as, when appropriate, the right to breed. All natural systems of property-tenure, however complicated, are essentially the same in that they depend entirely on conventional behaviour, and in that their effect is to limit the population-density without necessitating any resort to actual competition for food. *Competition for food itself* is what leads to overfishing, and what therefore tends to be eliminated by natural selection.

In birds, property-tenure can assume much more abstract or symbolic forms than the simple feeding-territory. As has just been indicated, by winning in competition a relatively small nest-site, a colonial bird can secure a right both to food and reproduction. Going a step further, symbolic forms of personal possession can be divorced altogether from real property, and come to apply to a purely abstract attribute, namely social status; and in sociable birds, as is well known, much energy may bepe snt in competing for and safeguarding relative standing in the social hierarchy.

These forms of substitute competition are closely interrelated. As far as exploiting food-resources is concerned, they have a common and important characteristic, namely that whenever the population-density tends to exceed the optimum they make it possible to remedy the situation by *nominating the actual individuals* which are to form the surplus. In competition for real property, such as territories, the

unsuccessful individuals are crowded out and forced to go elsewhere. When there is only sufficient of any commodity, such as food, for part of the population, those individuals standing too low in the social scale are excluded from sharing it. In every similar situation, in fact, a clear automatic distinction is made between those for whom the resources are sufficient, and those from whom they must be withheld. This again forms the basis of a general, self-regulating solution to the overfishing problem.

While it is necessary to oversimplify the working of the process slightly in this brief presentation, the underlying principle can clearly be seen. Competition between members of a population tends to be directed towards securing conventional situations serving as permits, of which the number has been restricted to the optimum by a process of natural selection. Only successful holders have the right to share in the resources of the habitat; and as long as their successful status is retained they may take whatever they need without restriction.

Though we have had in mind the exploitation by predators of their prey, the same principle is of universal application. It is very familiar in agriculture that overgrazing of pastures leads to their slow degradation; and in some parts of the Old World for instance the grazing of sheep and goats over to centuries has turned once-fertile land into a desert. Only under conditions of optimum exploitation can natural soil fertility be built up to the maximum level, such as appears to obtain under the undisturbed climax of vegetation.

This theory has the advantage of illuminating and unifying certain well known but previously disconnected phenomena. It offers the first general explanation of the function of peck-orders and similar social systems. Its ramifications can be shown to be unexpectedly wide throughout the whole realm of social behaviour. It points to the fact that in the evolution of social behaviour the advantage or survival of the social group readily takes precedence over that of the individual, and this in turn implies that, just as we commonly accept natural selection as working at the two levels of the species and the individual, so it must operate equally at the intermediate levels of inter-social or intergroup selection. The theory is also evidently related to the general phenomenon of the homeostasis or self-regulation of population-density, one aspect of which I presented at the last Congress at Basle in 1954 (Wynne-Edwards 1955). The further development of these topics must, however, await a subsequent publication.

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Das Problem des Reihens der Enten, besonders von *Anas strepera*

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Zur Definition: Das Reihen der Enten spielt sich etwa folgendermassen ab: Einem ♀ (ausnahmsweise 2 bis 3 ♀♀) folgen in der Luft 2 oder mehr ♂♂. Jedenfalls bildet mindestens 1 ♀ und gewöhnlich nur eines die Spitze oder den Mittel- und stets den Anziehungspunkt des reihenden Geschwaders. Für das Reihen ist aber nicht nur das Zahlenverhältnis der Geschlechter (Überwiegen der ♂♂) charakteristisch, sondern auch das fliegerische und stimmliche Verhalten von ♂♂ und ♀♀. Dieses nimmt sich auffallend anders aus als bei normalem Streichen, bei Platzwechselflügen oder gar auf dem Zug. Beim Reihen wird natürlich auch niemals die bekannte Winkelformation der Anatiden eingenommen. Die Anordnung und die Geschwindigkeit der einzelnen reihenden Enten wechseln ständig, oft im Bruchteil von Sekunden. Das alles ist bekannt und hierüber herrschen keine Meinungsverschiedenheiten.

Der Terminus »Reihen» sollte beibehalten werden. Er ist alteingebürgert und vorurteilsfrei, kurz und prägnant. Gerade weil wir nun wissen, dass das Reihen auch bei derselben Art, je nach Disposition und Stimmung oder auch Gelegenheit verschieden motiviert ist und verschiedenen Verlauf nimmt, brauchen wir einen neutralen Fachausdruck, der die komplizierten Vorgänge umfasst und das ihnen Gemeinsame hervorhebt. In diesem Punkt teile ich vollständig die Auffassung Baron Geyrs (1955) und kann mich nicht dem Vorschlag Lebrets anschliessen, den Terminus »Reihen» fallen zu lassen und stattdessen künftig von »Verfolgungsflügen» zu sprechen.

Es ist nicht meine Absicht, schon jetzt eine Lösung des ganzen Fragenkomplexes der sich an das Reihen knüpft, anzubieten oder auch nur zu versuchen. Dazu sind die Dinge viel zu verwickelt und die Lücken im Material zu gross. Wir sind uns ja noch nicht einmal über das reine Verhaltensinventar des Reihens der bekanntesten Schwimmenten im Klaren. Es ist aber an der Zeit, dass wir von unserem Ismaninger Standpunkt aus ebenfalls zu dem Problem Stellung nehmen, in der Hoffnung, wenigstens einen Schritt weiter zu kommen und einiges klären zu können, was unseres Erachtens in der Literatur bisher zu einseitig behandelt oder übersehen worden ist.

Im übrigen haben meine kurzen Ausführungen mehr programmatischen Charakter. Ich möchte sie als Anregungen und vorläufige Mitteilungen gewertet wissen, deren genauere, statistisch gefestigte Begründung z. Z. noch von meinem Schüler EINHARD BEZZEL und mir bearbeitet wird. Ausserdem beschränke ich mich hier im wesentlichen auf die Schnatterente, *Anas strepera*, die von den mir geläufigen Anatinen am häufigsten reiht, im Ismaninger Teichgebiet nächst der Stockente, *Anas platyrhynchos*, in grösster Dichte regelmässig nistet und deshalb ein gutes Objekt zur Lösung noch strittiger Fragen zu sein scheint.

Die Schnatterente r e i h t z u a l l e n J a h r e s z e i t e n. Eine Pause tritt bei uns nur in den rauhesten Monaten ein, ausser durch die dann herrschenden harten Lebensbedingungen vielleicht dadurch mitbedingt, dass nur ganz wenige Individuen hier überwintern. In manchen Wintern verschwindet die Schnatterente überhaupt ganz aus dem Ismaninger Teichgebiet. Dagegen tritt die im Juli theoretisch notwendige Unterbrechung des Reihens dadurch nicht mit der erwarteten Deutlichkeit und wochenlangen Dauer ein, dass die einzelnen ♂♂ mit einer Phasenverschiebung von einigen Wochen mausern, so dass die ersten Schlichtkleiderpel bereits wieder fliegen, wenn die letzten eben erst die Schwingen abgeworfen haben.

Die Neigung der Schnatterenten zur Geselligkeit untereinander und zu Gesellschaftsspielen der Erpel ist nach unseren Erfahrungen von Ismaning ausserordentlich gross. Bis in den Mai hinein und bereits wieder ab Juli konzentriert sich z. B. der Grossteil aller im Ismaninger Teichgebiet vorhandenen Schnatterenten, in der Grössenordnung von etwa 80 bis 200 Exemplaren, in einem einzigen der vielen gleichartigen Fischteiche. Wir befinden uns damit im Widerspruch zu der von K. LORENZ (1941 p. 269) geäusserten Ansicht. Schon im Juli beginnen die ♂♂, obwohl sie jetzt das Schlichtkleid tragen, ihre soziale Schwimmbalz. Diese geselligen Balzspiele, an denen sich auch feste Paare und hetzende ♀♀ beteiligen, erreichen schon im August einen gewissen Höhepunkt, also während der Ruhemauser der meisten ♂♂. Und nun wird auch gereiht.

1. B a l z f l u g oder F l u g b a l z. Sie findet von August, vielleicht schon Ende Juli, bis Anfang Mai statt und steht in innigem Zusammenhang mit der Schwimmbalz. Meist beginnt oder endet sie mit ihr oder es trifft beides zu. Man hat den Eindruck, dass die Flugbalz im wörtlichen und übertragenen Sinne einen Höhepunkt der Schwimmbalz bildet. Das heftig umschwärmte ♀ erhebt sich mitsamt den ♂♂ in die Luft, das ♀ gäkert dort ebenso wie vorher im Wasser, die ♂♂ lassen desgleichen unverändert ihr Grunzpfeifen (»Repp» = Grunzen nach der Terminologie von LORENZ und »Fiepen» = Pfeifen nach der Terminologie von LORENZ) vernehmen. Ernsthafte Beissereien finden dabei, wenigstens in der Regel, nicht statt. Oft sieht man, wie die ♂♂ den Hals S-förmig zurücklegen, »sich in die Brust werfen». Der sich ständig anders anordnende wirre Knäuel balzfliegender Schnatterenten bewegt sich laut und höchst erregt hin und her und in der Runde, mit geringer Eigengeschwindigkeit, durch die Luft. Von »Platzwechselflügen» kann man schon deswegen hier nicht reden, weil die Gesellschaft häufig den Platz gar nicht wechselt,

sondern an derselben oder an einer unwesentlich entfernten gleichartigen Stelle wieder einfällt. Wie erwähnt, wird dort nicht selten weitergebalzt. Ein äusserer, milieubedingter Anlass zum Auffliegen der Gesellschaft liegt wohl ebenfalls gewöhnlich nicht vor, mit Sicherheit dann nicht, wenn die vielen anderen Enten, aus deren Mitte sich der Balzklub erhebt, davon keine Notiz nehmen und ruhig weiterfressen oder -schlafen. Andrerseits werden im August oder September die umbalzten ♀♀ von den ♂♂ doch nicht ernsthaft bedroht, gebissen oder gar vergewaltigt. Ob man das kurz geschilderte Verhalten als »Balzflug« oder »Flugbalz« bezeichnen will, ist meines Erachtens nebensächlich. Einerseits handelt es sich um eine Flugart, die durch die Grunzpfifflaute und -bewegungen der ♂♂ und die doch wohl kokettierende Scheinabwehr der ♀♀ als Balzflug näher bestimmt ist, andrerseits kann man sie im Gegensatz zur Schwimmbalz als Balz in der Luft, also Flugbalz, auffassen. Es ist mir allerdings schwer verständlich, warum CHRISTOLEIT diese spätsommerliche und herbstliche Steigerung der Schwimmbalz auch von der Schnatterente nie erwähnte und VAUCHER (1954 p. 105) die von ihm trefflich geschilderten »parades nuptiales» »en vol» von der Schnatterente nur vom Frühjahr kennt. Wahrscheinlich versammeln sich in Ostpreussen und in den Dombes zur Hauptbalzzeit im August/September überhaupt keine so grossen Gesellschaften von *Anas strepera* wie im Ismaninger Teichgebiet. Auch kann die Art der Jagdausübung den Balzvorgang dann empfindlich stören und die Bildung von traditionellen Balzkonzentrationen verhindern. VAUCHER *(l. c.)* weist ausdrücklich auf die Schwierigkeit hin, sich vom August an, ein genaues Bild von den Schnatterentenpopulationen zu machen, weil die Jäger alles durcheinanderbringen.

Ein Unterfahren der ♀♀ durch einzelne ♂♂ und ein Vorausfliegen der ♂♂ kommt bei diesen Balzflügen vor, doch wohl zu selten, als dass man es als Flügelzeigen deuten könnte. Das oft beobachtete »Sichindiebrustwerfen» der Schnattererpel scheint mir eine in der Luft mehr oder weniger unvollkommen ausgefallene Grunzpfiffbewegung zu sein, bei der sich zugleich die Geschwindigkeit des fliegenden Vogels verringert. So erklärt sich möglicherweise das plötzliche Bremsen einzelner ♂♂. Ich möchte nicht behaupten, dass die Flugbalz ein »essentieller» Teil (v. GEYR) der Schnatterentenbalz ist. Zweifellos bilden Balzflüge aber oft den Höhepunkt der Erregung innerhalb der Schwimmbalz und mindestens ein Akzessorium des Balzgehabens. Ob man die Flugbalz als Ritualisierung der im Herbst sinnlosen Vertreibungs- und Hetzjagden deuten kann oder umgekehrt, muss ich vorerst dahingestellt sein lassen. Wie wenig diese Verhaltensweisen bisher bekannt sind, geht aus folgender Bemerkung LEBRETs (1955 p. 44) hervor: »Einmal hörte ich — im Oktober — von einem Schnattererpel während eines Verfolgungsfluges den »Grunzpfiff» (LORENZ *l. c.*), was ich bis dahin vom fliegenden Vogel für unmöglich gehalten hatte». Grunzpfiffe fliegender Schnattererpel vernahmen wir im Ismaninger Teichgebiet seit Jahrzehnten vielhundertmal. Offenbar ist aber der Stockerpel unfähig, im Flug zu pfeifen. Bei *Anas platyrhynchos* kommt Reihen als Fortsetzung der Balz in den Luftraum, echte Flugbalz, wenn überhaupt, dann sicher nicht als regelmässiger Teil der Balz

vor. Auch in diesem Punkte kann ich GEYR VON SCHWEPPENBURG nur zustimmen. Dagegen scheinen mir von den Anatinen mindestens K n ä k- *(Anas querquedula)* und S p i e s s e n t e n *(Anas acuta)*, vielleicht auch L ö f f e l e n t e n *(Spatula clypeata)*, Balzflüge durchzuführen, die denen der Schnatterente entsprechen. CHRISTOLEIT (1929), der die Enten so ausgezeichnet kannte und mit mancher Schlussfolgerung seiner Zeit weit voraus war, verallgemeinerte jedoch zu stark, wenn er meinte, Stock-, Schnatter-, Spiess- und Löffelenten verhielten sich in Bezug auf das Reihen wohl ziemlich gleich, Balzflüge gehören bei *strepera* zum Komment, bei *platyrhynchos* nicht. Baron GEYR (1955 p. 373) geht aber wiederum zu weit, wenn er schreibt: »Es gibt keine Flugbalz unserer Gründelenten!». Es bedarf hier kaum des Hinweises darauf, dass auch jahreszeitlich die Balz der Anatinenarten verschieden zu liegen kommt. Die Stockente beginnt erst lange nach der Schnatterente, die K r i c k e n t e gar erst im Laufe des Winters zu balzen. Trotzdem balzt, wie erwähnt, die Schnatterente auch noch im Frühling. Ferner sei hier bemerkt, dass wir Anlass zu dem Verdacht haben, dass es bei der Schnatterente Dauerpaare gibt, deren beide Gatten trotzdem bei der Gesellschaftsbalz mitmachen.

2. V e r t r e i b e n (= Revierfreihalten, Paarvertreiben) und V e r f o l g u n g s j a g d e n (= Hetzjagden, sexuell betont). Diese Arten des Reihens stehen seit Jahrzehnten im Mittelpunkt von Diskussionen, deren Kenntnis ich voraussetzen darf. Vertreibungs- und Verfolgungsflüge können naturgemäss nur zur Brutzeit im weiteren Sinne stattfinden, also wenn die Nistplätze bezogen, Gelege gezeitigt und bebrütet sowie die Jungen geführt werden. Beide unterscheiden sich von den Balzflügen unter anderem dadurch, dass ernsthaft gebissen oder der Versuch dazu gemacht wird. Die Tiere fliegen reissend schnell. Die ♀♀ werden offensichtlich wirklich bedroht und fühlen sich bedroht. Die ♂♂ versuchen hemmungslos das verfolgte ♀ zu fassen oder beissen sich gegenseitig in den Schwanz oder in die Beine und zwar sowohl der rechtmässige Mann den angreifenden Zudringling als auch umgekehrt. Das alles gibt es sicher bei *strepera*. Aber einerseits kommen bei der Schnatterente offenbar, wie gesagt, bis in den Mai hinein Schwimm- und Flugbalz vor, bei der die ♂♂ das ♀ respektieren und ihm nicht gefährlich auf den Leib rücken, andrerseits fragt es sich, ob man und wie man Vertreiben und Hetzen unterscheiden kann und soll. Mit Beginn der Gelegezeit, im Mai, ist die Balz zu Ende.

Statt von Revierfreihalten möchte ich lieber von P a a r v e r t r e i b e n sprechen, weil es vor allem (oder stets?) Paare sind, die den Angriff des ♂ eines überflogenen Paares auslösen und weil die Enten vielleicht überhaupt kein Nestrevier verteidigen. Die Nester der Enten haben oft nur geringen Abstand voneinander, während sich das Vertreiben über viele Hunderte von Metern erstrecken kann. Am 24. V.1954 beobachtete ich folgendes typische Vertreibungsmanöver, das als Beispiel für viele dienen möge: Ein ♂ reihte hinter einem Paar. Das verfolgende ♂ liess ab und fiel in »seinem» Teich ein. Das vertriebene Paar flog noch viermal diesen Teich an, jedesmal stieg das ♂ des schwimmenden Paares auf und griff das über dem Teich kreuzende Paar an. Ein ♂, vermutlich der Erpel des fliegenden Paares, biss dabei den

anderen in den Schwanz und einmal auch in das Bein. Schliesslich fiel das Paar, dem die Abweisungsversuche galten, aber doch in dem angestrebten Teich ein und wurde geduldet. Ähnliche Szenen sahen wir alljährlich in vielfacher Abwandlung. Die Jagden gehen gewöhnlich nur über wenige Teiche hinweg. Die etwa rechteckigen Teiche messen ungefähr 200 × 300 Meter und bilden eine rund 7 Kilometer lange Kette. In den meisten Fällen gelingt es wohl den Verteidigern, die Eindringlinge zu verscheuchen. Im einzelnen wäre an dem Vertreibungsverhalten noch vieles zu klären, z. B. in welcher Phase des Fortpflanzungszyklus, in welchem Bereich und wodurch (nur durch Paare?) es ausgelöst wird. Die Tatsache des regelmässigen Vertreibens von Paaren durch einzelne ♂♂ lässt sich aber nicht leugnen. Die Annahme eines AAM (angeborenen auslösenden Schemas) und auch dessen biologische Bedeutung liegen auf der Hand. Die Vögel, die mehr als Dreiviertel des Jahres in geselligem Verband leben, sollen während der Brutzeit möglichst verteilt werden. Diese These Baron Geyrs wird sich schwerlich widerlegen lassen.

Viel schwieriger sind die H e t z j a g d e n zu analysieren, von ihrer Bedeutung ganz zu schweigen. Es erfordert grosse Übung, den Vorgängen auch nur zu folgen und sie richtig zu protokollieren. Auch das Filmen und Photographieren ist wegen der unabsehbaren Weiträumigkeit der Szenerie und der Schnelligkeit der Bewegungen nicht leicht möglich und vom Glück und Geschick des Forschers abhängig. Bis jetzt kenne ich nur von der K o l b e n e n t e, *Netta rufina*, brauchbare Bilder zu unserem Thema, die G. A. Jauch 1953 veröffentlichte. Bei der Schnatterente sind typische Hetzjagden schon im März üblich, obwohl die Gelegezeit erst im Mai beginnt. So sah ich am 23. III. 1955 bis zu 6 ♂♂ mit 1 ♀ reihen. Nach dem Niedergehen aufs Wasser biss das ♀ die ♂♂, ausser sein »eigenes», ab, indem es immer wieder zum Angriff vorging. Das ♂ des Paares verhielt sich passiv, blieb aber stets an der Seite »seines» ♀. Übrigens bemerkte ich oft, dass das ♂ des Paares sich nicht weiter für sein ♀ einsetzte und nur alle Wendungen des ♀ mitmachte, wenn dieses massierten Balzereien fremder ♂♂ im Wasser oder in der Luft ausgesetzt war. Das ♀ verteidigte sich oft allein durch rasche Gegenstösse oder floh. Das zugehörige ♂ versuchte sich bei ihm zu halten.

Das Ende von Verfolgungs- und Vertreibungsflügen gestaltet sich nach unseren Ismaninger Beobachtungen an *strepera* recht verschieden. Oft umbalzen die ♂♂ das auf dem Wasser eingefallene ♀ heftig und in einer dem ♀ wahrscheinlich lästigen Weise. Ein andermal beruhigen sich die Tiere schnell und schwimmen friedlich umher, wie wenn nichts gewesen wäre, obwohl vielleicht kurz vorher die ♂♂ nach dem fliegenden ♀ gebissen haben. Umgekehrt fiel mir wiederholt auf, dass Paare und T r i o s (Weidmann 1956), die in lockerem Verband Nahrung suchend auf einem Teich umherschwammen, sofort unter Grunzpfiffen zu reihen begannen, wenn man sie aufgescheucht hat. Vergewaltigungen haben wir bei der Schnatterente im Ismaninger Teichgebiet niemals beobachtet. Sie kommen bei *strepera*, wenn überhaupt in freier Wildbahn, dann sicherlich nur ausnahmsweise vor. Wir haben den Eindruck, dass sich die Schnatterenten-♀♀ selbst im Frühjahr nicht nur gezwungen

zum Auffliegen entschliessen, sondern spontan die bis in den Mai verlängerten Balzereien veranlassen. Ich muss hier einfügen, dass im Ismaninger Teichgebiet bei den Schnatterenten das ganze Jahr über ein Erpelüberschuss besteht und dass man sehr oft Trios (♂♀♂) schwimmen oder fliegen sieht. Den Einwand, die Vergewaltigungsszenen würden uns auf den weiten, zum Teil zwischen den Dämmen verborgenen Wasserflächen leicht entgehen, können wir damit entkräften, dass wir von 8 bis 10 m hohen Warten aus hundertmal reihende Gruppen aufsteigen und auf dem offenen Spiegel einfallen sahen. Wir haben aber Grund zu der Annahme, dass auch bei der S t o c k e n t e unter völlig natürlichen Verhältnissen Vergewaltigungen weit seltener vorkommen als in Parks oder gar in Tiergärten, wo die Vögel mehr oder weniger domestizierenden Einflüssen ausgesetzt sind. Zu solchen Faktoren rechne ich Nahrungsüberfluss, grössere Sicherheit vor Feinden, unnatürliches Zahlenverhältnis der Geschlechter, geringe Individuenzahl und beschränkte Bewegungsfreiheit. Unter derartigen Umständen entfaltet sich das angeborene Verhalten nicht normal. Die wildlebenden Enten haben nicht so viel Zeit- und Kräfteüberschuss wie die halb- oder ganz zahmen, die sich ganz anders abreagieren können und müssen.

Zusammenfassend möchte ich betonen, dass es zunächst darauf ankommt, weitere genaue Beschreibungen über das Reihen zu sammeln, so dass es statistisch und tierpsychologisch ausgewertet werden kann. Wir stehen, zwar mit neuen Erkenntnissen und Hypothesen ausgestattet, doch noch am Beginn dieser Arbeit. Wenn das Verhaltensinventar des Reihens entwirrt ist, wie es HEINROTH und LORENZ durch vergleichendes Studium des übrigen Verhaltens der Anatinen weitgehend gelang, kann erwartet werden, dass auch von der ökologischen und psychologischen Bedeutung des Reihens der Enten ein klares und widerspruchsloses Bild entsteht.

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The Colonization of Coniferous Plantations by Birds

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During the past thirty years large areas of the uplands of Great Britain have been converted from heather moor (Callunetum), or *Nardus* or *Molinia* grassland, to coniferous forest, and as a result there has been a complete change in the avifauna, with a great increase in numbers both of species and of individuals. This paper is a preliminary report of observations that I have made during the breeding seasons of 1955—58 in six forests, all at or above 300 m. (1,000 ft) above sea level. The woods consist almost entirely of *Picea excelsa* and *P. sitchensis*, either in pure stands or in mixture, and are all at Longitude approximately 3°W. Two, in Cumberland, are at Latitude approximately 54°N, two, in Wales, at 52°N, and two, in Devonshire, at 50°N. The first and last groups are about 250 km. apart, and the Welsh forest about midway between them. The maps in the *Climatological Atlas of the British Isles* (Air Ministry: Meterological Office, 1952) suggest that while the Cumberland forests are rather colder in May and June, the mean temperatures of the Welsh and Devonshire forests are much the same. There are, however, differences concealed within this similarity of means; in Wales, for instance (as in Cumberland) May frosts are common, whereas in Devonshire the average date for the last Spring frost is about 15th April.

Except that gaps left where the original transplants have failed may be filled, the plantations receive little attention until they are about 15 years old, when they are »brashed», that is the side branches (which are now mostly dead) are cut off to a height of about two metres (six feet), and left lying on the ground. The height of the trees when this operation is carried out varies widely, but it is usually about five to seven metres (15 to 20 feet).

The density of the birds was estimated by means of the line transect (Yapp 1956). At all ages of forest, from bare moorland to those where the trees were 40 to 50 feet (12 to 15 metres) high, the total number of species recorded was 37 passerines and 12 non-passerines, but of these only 23 passerines and 11 non-passerines were at any time important in the community in terms of biomass. These numbers compare

with 39 passerines and 24 non-passerines recorded by TURČEK (1956) as important in the similar but older plantations of Czechoslovakia.

The unplanted moorland, and the plantations until the trees are one metre high, contain effectively two species only, the Skylark *(Alauda arvensis)* and the Meadow Pipit *(Anthus pratensis)*, with small numbers of carnivorous or parasitic non-passerines, Buzzard *(Buteo buteo)*, Kestrel *(Falco tinnunculus)* and Cuckoo *(Cuculus canorus)*. When the trees are between one and two metres high the Skylark and Meadow Pipit remain the commonest, but many other species appear. Some of these are birds which seem to prefer trees or bushes separated by shorter vegetation, such as the Linnet *(Carduelis cannabina)*, Yellowhammer *(Emberiza citrinella)*, Grasshopper Warbler *(Locustella naevia)*, Whinchat *(Saxicola rubetra)* and Stonechat *(S. torquata)*, but there are also some species characteristic of older woodlands, such as the Tree Pipit *(Anthus trivialis)*, Redpoll *(Carduelis flammea)*, Robin *(Erithacus rubecula)*, Chaffinch *(Fringilla coelebs)* and Willow Warbler *(Phylloscopus trochilus)*. By the time that the trees have grown to four metres, their side branches are touching and the original field layer of vegetation has been obliterated. Skylarks and Meadow Pipits have gone, and so have some of the bush species. At about four metres other tree-species, notably the Coal Tit *(Parus ater)*, Goldcrest *(Regulus regulus)*, Wren *(Troglodytes troglodytes)* and Woodpigeon *(Columba palumbus)* appear, and the community is virtually complete. Brashing has no sudden or marked effect.

The most interesting problem posed by these observations is the origin of the new birds, especially of the relatively rare transients. Grasshopper Warbler, Whinchat and Stonechat, for instance, are birds which are nowhere common in any natural or previously-existing semi-natural habitat in the British Isles, yet they sometimes appear suddenly in quite high density in these plantations. There are local variations; for example I have not yet recorded the Grasshopper Warbler from any Welsh or Devon forests, nor the Stonechat from those in Cumberland or Wales. It is difficult to account for these differences on climatic or general ecological grounds, and it may be that the appearance of a species in a new environment depends simply on the chance of there being surplus members of a neighbouring population to find and use it. If this is so, population control of these species would be by availability of suitable habitat; when the existing suitable area is filled, any individuals that are not accommodated in it must go elsewhere, and if they cannot find an appropriate environment they perish. Only occasionally, as when the Forestry Commission suddenly provides large areas of new plantation, is enough of the suitable habitat provided, and then there is an explosive spread of the species. Population control is not, in the usual sense of the term, density-dependent, but it is density-limited, in that there is a maximum density at which nests will be built. When the new areas of habitat are provided the population increases at a rate determined by the birth and death rates until a new steady state is reached. It is perhaps misleading to speak of population control; what is generally controlled is rate of change of population, and this is probably determined at any one time by a single limiting factor, in the sense in which

that term was defined by BLACKMAN (1905). Where the rate of change of population is held at zero by lack of suitable habitats a sudden new provision of these will allow expansion of population at a rate determined by whatever factor, such as availability of food, attacks of predators and so on, is now limiting.

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Birds Seen During the Excursions

The list below is compiled from data provided by Dr. G. Bergman (Archipelago), Dr. P. Nuorteva (Mainland), H. Ahlqvist, M. A. (Tvärminne), Dr. L. Siivonen and Prof. J. Koskimies (Lammi and Evo), P. Grenquist, M. A. (Snomu), Prof. E. Merikallio (Kuusamo), L. Lehtonen, M. A. (Kilpisjärvi), M. Rautkari, M. A. (Karigasniemi). + = observed, O = nest found, — = not observed.

	Archipelago near Helsinki	Mainland (Porvoo excursion)	Tvärminne	Lammi and Evo	Suomu	Oulu	Kuusamo	Kilpisjärvi	Karigasniemi
Gavia arctica	+	O	+	O	O	+	—	+	+
» stellata	—	—	—	O	+	+	—	+	+
Podiceps cristatus	+	O	+	O	—	+	—	—	—
» griseigena	—	—	O	O	—	O	—	—	—
» auritus	—	+	+	O	—	+	—	—	+
Phalacrocorax carbo	—	—	—	—	—	—	—	—	+
Anas platyrhynchos	+	+	+	+	O	O	—	—	+
» crecca	—	+	+	+	+	+	—	—	+
» querquedula	—	—	—	—	—	+	+	—	—
» penelope	—	+	—	—	+	O	—	+	+
» acuta	—	—	—	—	—	O	—	+	—
» clypeata	+	O	+	—	—	O	—	—	—
Aythya marila	—	—	—	—	—	O	—	+	—
» fuligula	+	+	+	—	+	O	—	+	+
» ferina	—	+	+	—	—	+	—	—	—
Bucephala clangula	+	—	+	O	O	O	O	+	—
Clangula hyemalis	+	—	—	—	—	+	—	+	O
Melanitta fusca	+	—	+	—	—	+	+	—	+
» nigra	—	—	—	—	—	+	—	+	+
Somateria mollissima	O	—	O	—	—	—	—	—	—
Mergus serrator	O	—	+	+	+	O	—	+?	+
» merganser	O	—	+	—	+	O	—	+?	—
» albellus	—	—	—	—	—	+	O	—	—
Anser anser	—	—	—	—	—	+	—	—	—
» fabalis	—	—	—	—	—	—	O	—	+
Cygnus cygnus	—	—	—	—	O	—	+	—	—
Aquila chrysaëtos	—	—	—	—	O	—	—	—	+
Buteo buteo	+	+	—	+	+	—	+	—	—
» lagopus	—	—	—	—	—	—	+	O	+
Accipiter nisus	+	—	—	+	+	—	—	—	—
» gentilis	—	—	—	O	+	—	(O)	—	—

	Archipelago near Helsinki	Mainland (Porvoo excursion)	Tvärminne	Lammi and Evo	Suomu	Oulu	Kuusamo	Kilpisjärvi	Karigasniemi
Milvus migrans	—	—	—	—	+	—	—	—	—
Pernis apivorus	+	+	—	—	+	—	—	—	—
Haliaëtus albicilla	—	—	—	—	—	—	+	—	—
Circus aeruginosus	—	+	—	—	—	+	—	—	—
» cyaneus	—	—	—	—	—	○	—	—	—
Pandion haliaëtus	+	○	○	○	○	+	○	—	+
Falco rusticolus	—	—	—	—	—	—	—	—	+
» subbuteo	+	—	+	—	○	+	—	—	—
» columbarius	—	—	—	—	—	—	—	+	○
» tinnunculus	+	—	+	+	+	+	—	+	+
Lagopus lagopus	—	—	—	—	—	○	—	○	○
» mutus	—	—	—	—	—	—	—	—	+
Lyrurus tetrix	○	+	+	○	+	—	—	—	—
Tetrao urogallus	—	+	—	○	○	—	○	—	—
Tetrastes bonasia	—	—	—	○	—	—	—	—	—
Grus grus	—	+	+	+	+	+	○	—	—
Fulica atra	—	+	—	—	—	+	—	—	—
Haematopus ostralegus	+	—	○	—	—	○	—	—	+
Vanellus vanellus	—	+	+	+	+	○	—	—	—
Charadrius hiaticula	+	+	○	—	—	○	○	+	○
» dubius	—	+	+	—	—	○	—	—	—
» morinellus	—	—	—	—	—	—	—	+	○
» apricaria	—	—	—	—	—	○	—	○	○
Arenaria interpres	○	—	○	—	—	○	—	—	—
Capella gallinago	—	+	+	—	+	○	○	+	+
Lymnocryptes minimus	—	—	—	—	—	+	+	—	+
Scolopax rusticola	+	—	—	—	—	—	—	—	—
Numenius arquata	—	+	+	+	+	○	—	—	—
» phaeopus	—	—	—	—	+	○	○	—	○
Limosa lapponica	—	—	—	—	—	—	—	—	○
Tringa ochropus	—	—	+	+	+	—	+	—	—
» glareola	—	—	+	—	—	○	—	○	+
» hypoleuca	+	+	+	○	○	+	○	+	+
» totanus	○	—	+	—	—	○	+	—	—
» erythropus	—	—	—	—	—	+	○	—	○
» nebularia	—	—	—	—	+	—	+	+	+
Tringa terek	—	—	—	—	—	○	—	+	—
Calidris temminckii	—	—	—	+	—	○	—	—	○
» alpina	—	—	—	—	—	—	—	+	+
Limicola falcinellus	—	—	—	—	—	—	○	—	○
Philomachus pugnax	—	—	—	—	—	○	○	—	○
Phalaropus lobatus	—	—	—	—	—	○	—	—	○
Stercorarius parasiticus	—	—	+	—	—	○	—	—	+
» longicaudus	—	—	—	—	—	—	—	+	○
Larus marinus	+	—	○	—	—	+	—	—	+

	Archipelago near Helsinki	Mainland (Porvoo excursion)	Tvärminne	Lammi and Evo	Suomu	Oulu	Kuusamo	Kilpisjärvi	Karigasniemi
Larus fuscus	O	+	O	+	+	O	—	—	—
» argentatus	O	+	O	—	+	O	—	+	+
» canus	O	+	O	+	+	O	—	+	+
» minutus	—	O	—	—	—	O	—	—	—
» ridibundus	+	O	O	+	+	O	—	—	—
Hydroprogne caspia	O	—	O	—	—	O	—	—	—
Sterna hirundo	O	+	O	+	+	O	+	—	—
» paradisaea	O	—	O	—	—	O	—	—	O
Alca torda	—	—	O	—	—	O	—	—	—
Cepphus grylle	+	—	O	—	—	O	—	—	—
Columba oenas	—	+	+	O	—	—	—	—	—
» livia domestica	—	+	—	—	?	+	—	—	—
» palumbus	+	+	+	+	—	—	—	—	—
Cuculus canorus	+	+	+	+	+	+	+	+	—
Bubo bubo	+	—	—	—	—	—	—	—	—
Surnia ulula	—	—	—	O	—	—	—	—	—
Strix aluco	+	—	—	O	—	—	—	—	—
» uralensis	—	—	—	O	—	—	—	—	—
Asio otus	—	—	—	—	+	—	—	—	—
» flammeus	—	—	—	—	—	O	O	—	—
Aegolius funereus	—	—	—	O	—	—	—	—	—
Caprimulgus europaeus	—	O	+	+	—	—	—	—	—
Apus apus	+	+	+	O	O	+	+	—	—
Picus canus	—	—	—	O	—	—	—	—	—
Dendrocopus major	—	+	—	O	O	—	—	—	—
» leucotos	—	—	—	O	—	—	—	—	—
» minor	—	—	—	+	—	—	—	—	—
Picoides tridactylus	—	—	—	O	—	—	O	—	+
Dryocopus martius	+	+	—	O	+	—	—	—	—
Iynx torquilla	—	+	+	O	+	O	+	—	—
Eremophila alpestris	—	—	—	—	—	—	—	+	+
Lullula arborea	—	—	+	—	—	—	—	—	—
Alauda arvensis	—	+	+	+	+	+	+	—	—
Riparia riparia	—	—	—	—	+	O	—	—	O
Hirundo rustica	+	+	+	+	O	O	+	—	—
Delichon urbica	+	+	+	+	O	O	+	O	—
Anthus trivialis	+	+	+	+	O	O	+	—	+
» pratensis	+	+	+	—	O	O	O	O	O
» cervinus	—	—	—	—	—	—	—	—	O
» spinoletta	—	—	+	—	—	—	—	—	—
Motacilla flava	+	+	+	+	O	+	O	O	O
» alba	+	+	+	+	O	+	+	+	O
Lanius collurio	—	—	+	+	+	+	—	—	—
» excubitor	—	—	—	—	+	—	—	—	O
Bombycilla garrulus	—	—	—	O	—	+	+	—	O

	Archipelago near Helsinki	Mainland (Porvoo excursion)	Tvärminne	Lammi and Evo	Suomu	Oulu	Kuusamo	Kilpisjärvi	Karigasniemi
Cinclus cinclus	—	—	—	—	—	—	—	○	○
Troglodytes troglodytes	—	—	—	+	+	—	—	—	—
Prunella modularis	—	+	—	○	—	—	+	+	—
Acrocephalus schoenobaenus	—	+	+	+	—	+	—	+	—
» scirpaceus	—	+	+	—	—	—	—	—	—
Hippolais icterina	—	—	+	+	+	—	—	—	—
Sylvia nisoria	—	—	+	—	—	—	—	—	—
» borin	+	+	+	+	+	+	—	—	—
» atricapilla	—	+	+	+	+	—	—	—	—
» communis	+	+	+	+	+	+	—	—	—
» curruca	+	+	+	+	+	+	—	—	—
Phylloscopus trochilus	+	+	+	+	+	○	+	+	○
» collybita	—	+	+	+	+	+	—	+	—
» sibilatrix	—	+	+	+	+	—	—	—	—
Regulus regulus	+	+	+	+	+	—	—	—	—
Ficedula hypoleuca	—	+	+	○	+	+	—	—	—
» parva	—	+	—	○	—	—	—	—	—
Muscicapa striata	+	+	+	○	○	○	+	—	+
Saxicola rubetra	—	+	+	+	+	+	—	—	—
Oenanthe oenanthe	+	+	+	+	+	+	+	+	+
Phoenicurus phoenicurus	—	+	+	○	○	+	+	○	○
Erithacus rubecula	+	+	+	+	+	+	—	—	—
Luscinia luscinia	—	—	—	+	—	—	—	—	—
» svecica	—	—	—	—	—	—	—	○	○
Turdus pilaris	+	+	+	○	○	+	○	○	○
» merula	+	+	+	+	+	—	—	—	—
» iliacus	—	+	+	○	○	+	○	+	○
» philomelos	+	+	+	○	○	+	○	—	+
» viscivorus	—	○	—	+	+	—	—	—	—
» torquatus	—	—	—	—	—	—	—	—	—
Parus montanus	+	—	—	○	+	+	+	—	—
» cinctus	—	—	—	—	—	—	+	—	○
» cristatus	+	+	+	○	+	+	+	—	—
» ater	+	+	+	+	—	—	—	—	—
» caeruleus	+	+	+	+	—	—	—	—	—
» major	+	+	+	○	+	+	+	—	○
Certhia familiaris	—	+	+	○	—	—	—	—	—
Emberiza citrinella	—	+	+	+	+	+	+	—	+
» hortulana	—	+	+	+	+	○	+	—	—
» rustica	—	—	—	+	+	+	○	—	—
» pusilla	—	—	—	—	—	+	—	—	—
» aureola	—	—	—	—	—	+	—	—	—
» schoeniclus	—	+	+	+	+	○	—	○	+
Calcarius lapponicus	—	—	—	—	—	—	—	+	○
Plectrophenax nivalis	—	—	—	—	—	—	—	+	○

	Archipelago near Helsinki	Mainland (Porvoo excursion)	Tvärminne	Lammi and Evo	Suomu	Oulu	Kuusamo	Kilpisjärvi	Karigasniemi
Fringilla coelebs	○	○	○	○	+	+	+	—	—
» montifringilla	—	—	—	○	+	+	+	○	○
Chloris chloris	—	+	+	+	+	—	—	—	—
Carduelis spinus	+	+	+	+	+	+	—	—	—
» carduelis	—	+	—	—	—	—	—	—	—
» cannabina	—	—	—	—	+	—	—	—	—
» flammea	—	—	—	○	+	+	○	○	○
» hornemanni	—	—	—	—	—	—	—	—	+
Carpodacus erythrinus	—	—	+	○	+	○	—	—	—
Pinicola enucleator	—	—	—	—	—	—	○	+	○
Loxia curvirostra	+	+	+	+	—	+	—	—	+
» pytyopsittacus	—	—	+	+	+	+?	—	—	—
Pyrrhula pyrrhula	—	+	—	+	+	+	—	—	—
Passer domesticus	—	+	+	+	+?	+	+	—	—
Sturnus vulgaris	+	○	+	○	○	○	—	—	—
Oriolus oriolus	—	—	—	+	+	—	+	—	—
Perisoreus infaustus	—	—	—	+	—	—	+	—	+
Garrulus glandarius	—	+	—	+	+	—	—	—	+
Pica pica	—	+	+	+	+	+	+	—	+
Corvus monedula	—	○	+	○	—	—	—	—	—
» corone cornix	○	○	+	+	+	○	+	—	+
» corax	—	—	(○)	○	+	○	+	+	○

A few rare birds observed in connection with the congress have been reported to the general secretary.

1. *Ardea cinerea*. One heron was seen flying over at Munksnäs, 2. 6. 1958. (L. v. HAARTMAN.)

2. *Chlidonias niger*. One bird was observed flying eastwards over the open sea in Kyrkslätt, 8. 6. 1958. (L. v. HAARTMAN.)

3. *Chlidonias niger*. »On 31st May, in late afternoon, four or possibly five Black Terns *(Chlidonias niger)* were observed near Otaniemi. They were seen against the light, at some distance; but their characteristic flight, black bodies and grey wings, were all noted; and they were flying in company with *Larus ridibundus* and *Sterna hirundo* (or. *S. macrura*); so their identification could not be doubted. At least one had been seen earlier in the afternoon by Dr. W. H. Thorpe and Mr. R. T. Peterson, independently.» (H. G. ALEXANDER.)

4. *Milvus migrans*. »On 1st June, at about 8.30 a.m., when I was standing near the main door of the buildings at Otaniemi, a large bird of prey came into view flying across the sky. I was able to get it into the field of my binoculars in the time to get the typical shape, especially the slightly forked tail, and dark colour, of a Black Kite *(Milvus migrans)*.» (H. G. ALEXANDER.)

5. *Lanius collurio*. »On June 16th, on excursion from Oulu, some forty (?) miles to the south-west, from the bus I observed what appeared to be a Redbacked Shrike *(Lanius collurio)*. Although I was fairly confident that is was not *L. excubitor*, I might not have been ready to record it definitely on my own observation alone; but I found that it had been well seen also by another British ornithologist, who was on the side of the bus nearest to it, whereas I was on the wrong side of the bus.» (H. G. ALEXANDER.)

6. *Acrocephalus arundinaceus*. Observed 4.6. on the ship Stockholm–Helsinki one and a half hours from Helsinki (D. HUESTIS SPEIRS, Toronto Field Naturalists' Club, Newsletter 159, October 1958).

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[1] We are indebted to Dr. FINN SALOMONSEN for valuable aid in respect to the nomenclature.

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2. *Emberiza aureola*. Female. Liminka 8. 7., 1956. (N. Fritzén.)

1. *Emberiza aureola*. Male. Liminka 8. 7., 1956. (N. Fritzén.)

3. Tringa terek. Islet not far from Oulu 26. 6., 1957. (N. Fritzén.)

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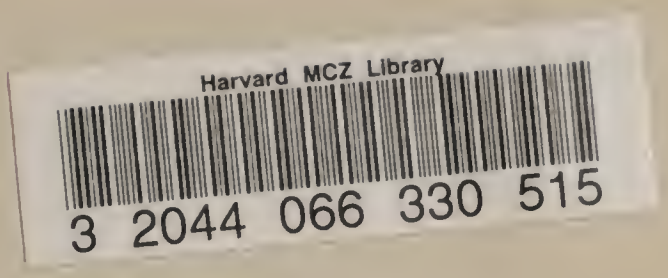

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